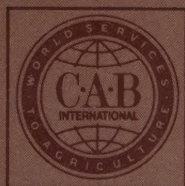


HYMENOPTERA AND BIODIVERSITY



Edited by
John LaSalle
Ian D. Gauld

The Natural  History Museum



Donet Agosh

London

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Preface

A great deal of attention has been focused on biodiversity over the last several years, and a variety of convincing arguments have been put forward to justify the preservation and conservation of the world's plant and animal species. There are those who feel that all species have the right to continued existence without threat of extinction. Others offer financial reasons why we should conserve and survey biodiversity. Our unknown biological resources could contain species which are potentially important for food or medicine. One could also argue that almost any extinctions are detrimental because a species cannot be removed without affecting other organisms, and the present extinction pulse must be having an adverse effect on the overall ecological balance of the planet.

But having reached the important conclusion that it is necessary to preserve biodiversity, there are still several difficult decisions to be made. We do not have the resources to preserve, conserve, inventory and study all the world's species, so we must choose areas of greatest importance on which to concentrate our attention. If we wish to preserve diversity, we must focus our studies on groups which are important to maintaining diversity in other groups. It is not just that some groups are more diverse than others; certain groups have a greater influence on diversity in other organisms. It is also imperative to discover which groups have the greatest impact on maintaining diversity, and focus particular attention on them.

Hymenoptera is such a group. It not only forms a major component of diversity in itself, it is vital in sustaining diversity in other groups. How do Hymenoptera species promote diversity in other groups? They are absolutely essential to sustaining diversity in plants. They are one of the most important groups of pollinators; they are a major group of seed dispersers; they protect

plants from a multitude of herbivores which would ravage them without some measure of control. They can regulate population size of arthropods. This not only protects plants but also permits diversity within arthropod groups by controlling dominant competitors which would exclude other species in the absence of some control. They even supply resources necessary to the survival of many vertebrate species. Unfortunately, it appears that Hymenoptera is an extinction prone group, and many species are particularly susceptible to environmental disturbances.

This volume attempts to examine the following questions. How do species of Hymenoptera affect diversity in other organisms? Is Hymenoptera an extinction prone group? If Hymenoptera species are differentially removed from terrestrial ecosystems, what will be the consequences? The first chapter gives an introduction to the volume, and explores these questions in greater depth.

Intraspecific diversity and the level of genetic variation present in Hymenoptera is considered in Chapter 2. Aspects of hymenopteran genetic systems result in less intraspecific genetic variation than in other insect groups, and this has implications both for conservation and for biological control.

Chapters 3 and 4 document the decline in aculeate bees and wasps due to habitat degradation in Central America and South Africa. Due to resource partitioning in food or nesting requirements, the destruction of microhabitats can have drastic effects on diversity of species present.

Chapters 5 through 11 provide examples of the importance of Hymenoptera in both natural and agricultural ecosystems. Chapter 5 discusses the ant mosaics, and how they affect arthropod diversity. Chapters 6 and 7 focus on bees in natural and agricultural environments, and point out the importance of a high diversity of bees in maintaining high plant diversity.

Chapters 8 through 11 treat the largest group of Hymenoptera, the parasitic Hymenoptera. They discuss the importance of this group to natural and agricultural ecosystems, the complex of interactions they have with other species, reasons for the high diversity of species, and methods for enhancing the diversity of parasitic Hymenoptera in agricultural ecosystems.

Chapter 12 looks at patterns in the descriptions and richness of Hymenoptera, and points out that the best known areas are often those with the least diversity.

Chapters 13 through 15 look at biodiversity as a whole, and different ways to approach the problems associated with trying to survey, identify and study the world's diversity. Chapter 13 shows that the needs of developing nations might not always be the services that taxonomists in developed countries most want to provide.

How does one measure diversity, and can one type of diversity be more important than another? Chapter 14 looks at methods for quantifying and measuring diversity, and discusses the value of being able to discriminate between different types of diversity.

And how does one conserve and study biodiversity? Chapter 15 discusses the

programme currently underway in Costa Rica for the study of tropical biodiversity.

This is the first volume to concentrate on justification for a specific group that is important in preserving biodiversity. We have not covered all of the multitude of aspects of Hymenoptera biology and ecology that make them important. This would be an overwhelming task and outside of the remit of this volume. We are pleased that so many of the authors contributed such extensive bibliographies; these will provide readers with access to the enormous literature on various aspects of Hymenoptera.

It is tempting for us as editors to make specific recommendations based on the information in this volume. We are both systematists, and our original intention was to compile evidence to support increased systematic research on Hymenoptera. But during the course of this work we realized that there are many valuable and necessary areas of research on Hymenoptera, and information found in this volume can serve to justify all of them.

It will require a great deal of work to survey, describe and begin to understand the biology of the Hymenoptera. If one looks at the Hymenoptera as an essential element in our struggle to maintain ecological balance on the planet, then one can see that efforts spent on gaining knowledge of Hymenoptera are well invested.

The applied biological control of a variety of insect pests has provided direct evidence of the importance of Hymenoptera, and leaves us with a final, and extremely important, justification for conserving biodiversity. By preserving the diversity present in terrestrial ecosystems, we are maintaining a pool of potential biological control agents, and retaining the ability to control tomorrow's pests in a manner that is both economically and environmentally sound. Without the option for biological control, we will be forced to use pest control measures which will surely accelerate the current decline in environmental quality.

John LaSalle
Ian D. Gauld
London, 1992

Hymenoptera: Their Diversity, and Their Impact on the Diversity of Other Organisms

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Introduction

No matter how one chooses to measure diversity, Hymenoptera is an extremely diverse group. The morphological diversity of Hymenoptera is reflected in the fact that Hymenoptera alone of the major insect orders has no unifying common name. Coleoptera are beetles, Lepidoptera are moths and butterflies, Diptera are flies, but the Hymenoptera are wasps, bees, ants and sawflies. Although certain hymenopterans such as ants and bees are among the most widely recognized of insects, many people are unaware that they are close relatives, and that together they comprise only a fraction of an order that is dominated numerically by a multitude of parasitic species.

There are currently over 115 000 described species of Hymenoptera. To put this in perspective: there are over twice as many species of Hymenoptera as there are of all terrestrial and aquatic vertebrates put together; twice as many species of ants as mammals; more species of bees than fishes; and more species in a single family of parasitic Hymenoptera (the Ichneumonidae) than birds and mammals put together (figures from Wilson, 1988; Gaston, this volume Chapter 12). But, unlike vertebrates, the majority of species of Hymenoptera are yet to be described, and furthermore many of those species that are described are not currently recognizable.

Although estimates for the actual numbers of Hymenoptera can vary widely (see Gaston, 1991; LaSalle and Gauld, 1992), it is clear that they are one of the major components of insect diversity. Hymenoptera appear to be the most species rich of the insect orders in several temperate regions (Gaston, 1991); and

studies by Stork (1991) in Borneo also found Hymenoptera to be the most diverse order represented.

Hymenoptera species are diverse biologically also. Members can be phytophagous, entomophagous, or a combination of both. Entomophagous members can be predatory or parasitic, with a variety of intermediate biologies that defy precise classification. Eusociality has reached its pinnacle in the Hymenoptera. Ant societies have complex social organization, and preceded humans in the development of agriculture, slave-making and the domestication of other species. The Hymenoptera contains more beneficial species than any other insect order. They are of direct economic importance in the biological control of agricultural or forestry pests, the pollination of flowering plants and the production of commercial products such as honey and wax.

Perhaps more important than their economic value is their environmental value. Hymenoptera are a vital component of all terrestrial ecosystems. Ants can be seen to dominate ecosystems in a way unequalled by any other organism. In addition to their sheer biomass, a multitude of mutualistic ant-plant associations are known which ensure the survival of many plant species, and ant mosaics are formed in which dominant ant species can not only affect and control the distribution of non-dominant ant species, but also influence both the species composition and abundance of other arthropod taxa. Bees are the primary pollinators of angiosperms in many areas, and constitute the most diverse group of flower-visiting insects in these areas; without a high diversity of bees, the diversity of plants would surely decline. And many species of Hymenoptera which develop as parasitoids or predators of a wide range of other insects have a role in the natural regulation of populations of phytophagous insects.

Yet, despite their seeming success, Hymenoptera appear to be a fragile group when confronted with the environmental degradation that is now occurring. Evidence presented in this volume indicates that many groups of Hymenoptera are extinction prone, and we are entering a period of mass extinctions. We predict that the differential removal of Hymenoptera from natural ecosystems will cause a cascade effect which will result in even more rapid and irreversible environmental decline than we are presently facing.

The Order Hymenoptera – an Overview

The taxonomy and general biology of the Hymenoptera is summarized in Table 1.1. Although different authors have different ideas on the higher classification, there are presently about 80 families recognized. The Hymenoptera is composed of two suborders: the Symphyta and the Apocrita.

The Symphyta, or sawflies, are the most primitive members of the order. They have the most complete wing venation, and they do not have the constricted 'wasp-waist' seen in the rest of the order. Most species have phytophagous larvae and have much the same lifestyle as Lepidoptera. This is a

Table 1.1. Families of Hymenoptera, with common names and principal modes of development.

Taxa	Common name	Mode of development
Suborder Symphyta	Sawflies and horntails	
Xyeloidea		
Xyelidae	no common name	phytophagous
Megalodontoidea		
Pamphiliidae	leaf-rolling and web-spinning sawflies	phytophagous
Megalodontidae	no common name	phytophagous
Tenthredinoidea		
Blasticotomidae	no common name	phytophagous
Argidae	no common name	phytophagous
Cimbicidae	no common name	phytophagous
Diprionidae	conifer sawflies	phytophagous
Tenthredinidae	common sawflies	phytophagous
Pergidae	no common name	phytophagous
Siricoidea		
Siricidae	horntails	phytophagous
Xiphydriidae	wood wasps	phytophagous
Anaxyelidae	incense-cedar wood wasps	phytophagous
Orussoidea		
Orussidae	parasitic wood wasps	parasitoid
Cephoidea		
Cephidae	stem sawflies	phytophagous
Suborder Apocrita		
<i>Parasitica</i>	Parasitic Hymenoptera	
Trigonalypoidea		
Trigonalypidae	no common name	parasitoid
Megalyroidea		
Megalyridae	no common name	parasitoid
Evanioidea		
Evanidae	ensign wasps	parasitoid
Aulacidae	no common name	parasitoid
Gasteruptionidae	no common name	parasitoid
Stephanoidea		
Stephanidae	no common name	parasitoid
Ceraphronoidea		
Megaspilidae	no common name	parasitoid
Ceraphronidae	no common name	parasitoid
Proctotrupoidea		
Pelecinidae	no common name	parasitoid
Vanhornidae	no common name	parasitoid
Ropronidae	no common name	parasitoid

Table 1.1 continued

Taxa	Common name	Mode of development
Peradeniidae	no common name	not known
Heloridae	no common name	parasitoid
Austroniidae	no common name	parasitoid
Monomachidae	no common name	parasitoid
Proctotrupidae	no common name	parasitoid
Diapriidae	no common name	parasitoid
Platygasteroidea		
Scelionidae	no common name	parasitoid
Platygasteridae	no common name	parasitoid
Cynipoidea		
Ibaliidae	no common name	parasitoid
Liopteridae	no common name	parasitoid
Figitidae	no common name	parasitoid
Eucoilidae	no common name	parasitoid
Cynipidae	including gall wasps	phytophagous, parasitoid
Charipidae	no common name	parasitoid
Chalcidoidea		
Leucospidae	no common name	parasitoid
Chalcididae	no common name	parasitoid
Eurytomidae	including seed chalcids	parasitoid, phytophagous
Torymidae	no common name	parasitoid, phytophagous
Aganidae	fig wasps	phytophagous
Ormyridae	no common name	parasitoid
Eucharitidae	no common name	parasitoid
Perilampidae	no common name	parasitoid
Pteromalidae	no common name	parasitoid
Eupelmidae	no common name	parasitoid
Tanaostigmatidae	no common name	phytophagous
Encyrtidae	no common name	parasitoid
Tetracampidae	no common name	parasitoid
Aphelinidae	no common name	parasitoid
Signiphoridae	no common name	parasitoid
Eulophidae	no common name	parasitoid, phytophagous
Elasmidae	no common name	parasitoid
Trichogrammatidae	no common name	parasitoid
Rotoitidae	no common name	not known
Mymaridae	fairyflies	parasitoid
Mymarommatidae	no common name	not known
Ichneumonoidea		
Ichneumonidae	no common name	parasitoid
Braconidae	no common name	parasitoid

Table 1.1 continued

Taxa	Common name	Mode of development
<i>Aculeata</i>	Bees, Ants, ¹⁴ /asps	
<i>Chrysidoidea</i>		
Plumariidae	no common name	parasitoid
Scolecbythidae	no common name	parasitoid
Sclerogibbidae	no common name	parasitoid
Dryinidae	no common name	parasitoid
Embolemyidae	no common name	parasitoid
Bethylidae	no common name	parasitoid
Chrysididae	cuckoo wasps	parasitoid
<i>Vespoidea</i>		
Tiphidae	no common name	parasitoid
Mutillidae	velvet ants	parasitoid
Sapygidae	no common name	parasitoid
Scoliidae	no common name	parasitoid
Bradyobaenidae	no common name	not known
Sierolomorphidae	no common name	not known
Rhopalosomatidae	no common name	parasitoid
Formicidae	ants	predator, phytophagous
Pompilidae	spider wasps	predator
Vespidae	including paper wasps, yellow jackets, hornets, mason wasps, potter wasps	predator
<i>Apoidea</i>		
Sphecidae	including mud daubers, sand wasps, bee wolves, cicada killers	predator
Apidae	bees	pollen (plus nectar or oil) feeders

relatively small group, consisting of 14 families which contain just over 5% of described Hymenoptera species, with the majority of them in the family Tenthredinidae (Gaston, this volume Chapter 12).

The Apocrita contains the vast majority of Hymenoptera. It is divided into two groups: the Parasitica (=Terebrantes) and the Aculeata. The aculeates represent the most derived group of the Hymenoptera, in which the ovipositor structure has been modified into a sting. This group contains the types of Hymenoptera which would be recognized by most people, such as bees, wasps, hornets and ants. Species can be quite large; certain spider wasps in the genus *Pepsis* (Pompilidae) have a wingspan of up to 10cm and provision their nests with tarantula spiders (C.R. Vardy, pers. comm.). The majority of species are

predatory (wasps, hornets) or pollen feeding (bees), however parasitism is common, particularly in the lower aculeates (Chrysidoidea). The Aculeata alone of the three major divisions within the order represents a monophyletic assemblage. There are 19 families of Aculeata, which hold a little over 45% of described Hymenoptera species (Gaston, this volume Chapter 12), with the families Apidae (bees), Formicidae (ants) and Sphecidae containing the most species. There is some controversy concerning the number of aculeate families; we have treated all bees as belonging to the single family Apidae, although other authors recognize up to 12 families of bees (O'Toole and Raw, 1991).

The final, and largest, group of Hymenoptera is the Parasitica. This is a loosely defined group which includes all non-aculeate Apocrita. Members are those hymenopterans which have a constricted waist, but in which the ovipositor has not been developed into a sting. The vast majority of species are parasitoids, however there are species which are phytophagous, gall-formers, or predators. The Parasitica contains 48 families in 10 superfamilies, which include almost half of described Hymenoptera species; with most of the species in the superfamilies Ichneumonidae and Chalcidoidea (Gaston, this volume Chapter 12). Although this is the largest group of Hymenoptera, and may eventually be shown to contain 75% of the species, the majority are quite small and most people are unaware of their existence. Indeed, the smallest of all insects may be parasitic Hymenoptera. Species in the genus *Megaphragma* (Trichogrammatidae) are parasitoids within the eggs of thrips, and the adult wasps may be no more than 0.18 mm in length (Doutt and Viggiani, 1968). The small size and poor state of knowledge of most parasitic Hymenoptera groups is reflected in the fact that very few have common names (see Table 1.1).

Further information on the classification, biology and importance of Hymenoptera can be found in a variety of regional works, such as Scholtz and Holm (1985), Gauld and Bolton (1988), Borror *et al.* (1989), Gauld *et al.* (1990), and Naumann (1991).

Diversity within Hymenoptera

Diversity occurs at three levels: gene, species and ecosystem (see Reid and Miller, 1989; Solbrig, 1991b). At the species and ecosystem levels, Hymenoptera are among the most diverse and important of all organisms. Not only are Hymenoptera one of the most species rich insect orders, they are also incredibly diverse in the biology displayed by those species. Hymenoptera can be found in large numbers in almost any terrestrial ecosystem, and more importantly, they are responsible for a larger share of interactions with other species in ecosystems than any other insect group. In contrast, Hymenoptera species display less genetic diversity than that found in most other insects, and this can adversely affect their chances for survival.

Diversity at the gene level

Genetic diversity in Hymenoptera, along with the implications of this diversity to conservation and biological control, is discussed by Unruh and Messing (this volume Chapter 2). They point out that genetic diversity in Hymenoptera is less than that found in most other insects. This has ramifications in terms of conservation biology, as lower genetic diversity results in an increased minimum viable population size in Hymenoptera which makes them more sensitive to environmental perturbations. However, this increased sensitivity means that Hymenoptera would be better candidates as indicator species for monitoring environmental disturbances. Lower genetic variation has other implications, because genetic variation has been seen on several occasions to be important to biological control. An in-depth treatment of genetic diversity within Hymenoptera is given by Unruh and Messing (this volume Chapter 2).

Diversity at the species level

Numbers of species

Hymenoptera is one of the four largest insect orders (the other three are Coleoptera, Diptera and Lepidoptera). In terms of described species, Coleoptera and Lepidoptera are both more diverse than Hymenoptera (Arnett, 1985). However, there is mounting evidence to indicate that Hymenoptera may be the largest order of insects. By examining various estimates of total numbers of species (described and undescribed) Gaston (1991) concluded that Hymenoptera is clearly the most diverse order in several temperate regions.

Precise estimates for tropical regions are not available. However, studies in these regions indicate that Hymenoptera are as diverse in the tropics as they are in temperate regions. Stork (1991) found that Hymenoptera was the most species rich group in tree canopies in tropical forest in Borneo, and they accounted for just over 25% of arthropod species.

Several recent works have examined in great detail the numbers of described species of insects (Arnett, 1985; Gaston, 1991), numbers of estimated species of insects (Erwin, 1982, 1983; Hodkinson and Casson, 1991, Holloway and Stork, 1991) and numbers of described and/or estimated species of Hymenoptera (Brown, 1982; Gauld and Bolton, 1988; Masner, 1990; Gaston, this volume Chapter 12). It is sufficient for the purposes of this chapter to summarize all the above mentioned works into a single sentence: the order Hymenoptera is very large, very important and very poorly known.

Biology

We are not going to include a comprehensive section on all aspects of Hymenoptera biology; that is not the purpose of this chapter. Simply reading this and other

chapters in this volume will give some idea of the fascinating variety of lifestyles in the Hymenoptera. We include this section to remind people that diversity in biology is an important and often overlooked aspect of species level diversity. A great deal of attention has been placed on number of species as an indication of diversity, but the significance of diversity is in what species do. The reason Hymenoptera are important is because they are as diverse in biology as they are in numbers of species.

Diversity at the ecosystem level

Numbers of individuals

If number of individuals is an indicator of ecological importance, ants are clearly one of the most dominant groups of organisms on land. Wilson (1990) discussed the importance of social insects, and presented evidence on their importance in ecosystems. He pointed out that in Brazilian tropical forest, the biomass of ants is approximately four times greater than that of the entire vertebrate fauna combined, and the biomass of all social insects, including ants, social wasps, bees and termites is about seven times the vertebrate fauna. In a rain forest near Manaus, Brazil, Hymenoptera (ants, stingless bees and social wasps) accounted for just under half of the total insect biomass, with the biomass of stingless bees and social wasps alone about equal to that of all beetles (Fittkau and Klinge, 1973; Wilson, 1990). Ants are also abundant in temperate zones: in Finland it has been estimated that ants account for 10% or more of the entire animal biomass of the Tvarminne Archipelago (Wilson, 1990). Studies by Stork (1991) showed that in fogging samples from tree canopies in Borneo, Hymenoptera accounted for 27.8% of all arthropod individuals collected.

In contrast, parasitic Hymenoptera are often present in high numbers of species, but low numbers of individuals. However, population size in parasitoid species which can regulate the population size of another species in a density dependent manner is not in itself a clear indication of the importance of that parasitoid in the ecosystem (LaSalle and Gauld, 1992; LaSalle, this volume Chapter 8).

Trophic interactions

A strong indication of the importance of Hymenoptera is found in the number of trophic interactions they represent in terrestrial ecosystems. One example of this is the parasitic Hymenoptera. Most insect parasitoids are Hymenoptera, and food chains comprising green plants, insect herbivores and parasitoids contain over half of all known species of metazoans (Price, 1980; Strong *et al.*, 1984; Hawkins and Lawton, 1987; see Hawkins, this volume Chapter 10). It has been estimated that a typical phytophagous species is attacked by 5–10 species of parasitoids; this pattern seems to hold true for both temperate and tropical

regions (May, 1988, based on data from Hawkins and Lawton, 1987). A separate study showed that hymenopterans as predators and parasitoids interact with more numbers of insect prey than any other insect order in terrestrial habitats, and that they account for 57% of all insect predation on other insects (Schoenly, 1990). In addition to predator links, Schoenly (1990) found that Hymenoptera also accounted for the highest number of prey links (about 44%).

The magnitude of the numbers of certain ant species makes any interactions they have important. An ordinary colony of *Formica polyctena* collected about 6 million prey items per year from a one-third hectare plot; one colony of *F. rufa* was observed to take 21 700 sawfly larvae and moth caterpillars in a single day (Hölldobler and Wilson, 1990, and references therein). Leafcutter ants in the New World tropics consume more vegetation than any other group of comparable taxonomic diversity, including mammals, homopterans and lepidopterans (Hölldobler and Wilson, 1990). The amount of vegetation that *Atta* leafcutting ants alone cut from Neotropical forests has been calculated from a range of studies to lie between 12 and 17% of total leaf production (Cherrett, 1986, 1989).

Another trophic interaction is the gathering of flower produced pollen, nectars and oils, an activity that forms the basis of angiosperm pollination. In many areas of the world, bees are the primary pollinators of angiosperms, and constitute the most diverse group of flower visiting insects (Neff and Simpson, this volume Chapter 6). The number of individual interactions by pollinating bees can be enormous; it has been estimated that to produce a single gram of honey, the bumblebee *Bombus fervidus* visits over 200 000 red clover florets (Heinrich, 1979).

How Hymenoptera Affect Diversity in Other Organisms

In this section we will limit our examples to three main groups of Hymenoptera: ants, bees and parasitic Hymenoptera, as we feel that these groups have the largest impact on other organisms and the maintenance of diversity. This is not to say that other groups of Hymenoptera are not important, or do not contain keystone species. For example, Raw (1988) showed that a complex of social wasps (Vespidae) were able to provide biological control of several pests in native 'shifting cultivation' agricultural systems in Brazil. A high diversity of these wasps is important, because the efficiency of the various species differed depending on conditions (such as size and age of the clearings and density of vegetation).

Similarly, we cannot begin to describe all the ways that ants, bees and parasitic Hymenoptera influence other organisms; we have chosen examples from within these groups which best illustrate the points we wish to make. Since much of the attention in conservation biology has centred on vertebrates and plants, we have specifically chosen examples which demonstrate ways in which

Hymenoptera contribute to the maintenance of diversity in these groups. However, it should be remembered that these are just some examples of the effect of Hymenoptera on other organisms, and that hymenopterans have an equal (if not greater) effect on other arthropods than they do on macro-organisms (see Majer, this volume Chapter 5; LaSalle, Chapter 8; Memmott and Godfray, Chapter 9; Hawkins, Chapter 10; Altieri *et al.*, Chapter 11).

Keystone species

Not all species have the same influence in an ecosystem. Species that have disproportionately large influence on the character or structure of an ecosystem are called keystone species (Reid and Miller, 1989; Solbrig, 1991b). When keystone species are lost, removed, or have their activities disrupted, there is a noticeable effect on the system that is termed cascade effect. Solbrig (1991b) discussed three main categories of keystone species:

1. predators, parasitoids, herbivores and pathogens that contribute to the maintenance of diversity by reducing the abundance of dominant competitors and thus prevent competitive exclusion;
2. mutualists (partner species whose fates are linked);
3. species that provide resources which are critical to the survival of dependent populations.

Table 1.2. Examples of keystone categories in which Hymenoptera contribute to the diversity of other organisms. All examples are discussed in text.

	Ants	Bees	Parasitic Hymenoptera
Keystone predators and parasitoids	ants as predators		parasitic Hymenoptera as parasitoids
Keystone mutualists	ant-plant mutualisms	bees as pollinators	fig wasps as pollinators
Keystone resource species	ants and soil composition ants which provide resources for vertebrates		
Keystone dominants	ant mosaics		

Ant mosaics are a striking example of species with the ability to influence both the structure and the character of an ecosystem, and they are a major contributing factor to tropical diversity. However, dominant ants do not readily fit into any of the keystone categories mentioned by Solbrig above, so we are using the category of keystone dominants to contain these species (see below).

Table 1.2 lists some examples of Hymenoptera which belong to these keystone categories. They are discussed more fully below.

Keystone predators and parasitoids

Predators and parasitoids become important for the maintenance of diversity when they regulate the populations of species which would otherwise out-compete, and thus eliminate, other species. Although predators and parasitoids basically operate in the same manner, there are differences between them which justify the recognition of the distinction between these two categories (LaSalle and Gauld, 1992).

The Hymenoptera parasitoids

Parasitic Hymenoptera play a major role in the balance of terrestrial ecosystems through their ability to regulate populations of phytophagous insects (LaSalle and Gauld, 1992; LaSalle, this volume Chapter 8). By limiting the population size of a species that would otherwise outcompete other species, parasitoids can not only help maintain high species diversity in herbivores, they can prevent herbivores from decimating their plant hosts. Additionally, community interactions involving parasitoids appear to be more stable than those involving predators (Toft, 1986; Pimm and Lawton, 1978; see LaSalle, this volume Chapter 8).

Examples of the importance of parasitic Hymenoptera can be found from biological control projects. Removal of one or a few species of parasitoids from an area under biological control can result in massive resurgences in pest populations, and these can eventually result in the exclusion of other phytophagous species and even defoliation or death of plants. With perhaps several hundred thousand species of parasitic Hymenoptera, one can assume that many herbivorous insects in natural ecosystems are held under similar levels of control. Further discussion of the importance of parasitic Hymenoptera can be found in LaSalle and Gauld (1992) and LaSalle (this volume Chapter 8).

Ants as predators

The predatory powers of ants have been known for centuries. The weaver ant, *Oecophylla smaragdina*, is the earliest known biological control agent, and nests of this ant were sold in markets near Canton as early as 300 BC. Farmers placed the nests in citrus groves for control of beetle larvae and caterpillars. Movement within the groves was facilitated by the placement of bamboo bridges to connect

the trees (DeBach and Rosen, 1991). We have already mentioned the enormous numbers of prey which can be taken by *Formica* species. They were so effective at protecting mountain birch trees against an outbreak of *Oporinia autumnata* (Geometridae), that areas around the *Formica* colonies could be seen as green areas of intact trees 40 metres in diameter remaining in a mostly grey, defoliated forest (Hölldobler and Wilson, 1990, and references therein).

Keystone mutualists

Keystone mutualists are particularly worthy of mention in Hymenoptera. In highly co-evolved and mutually beneficial interactions the loss of one species will more than likely cause the loss of the second. Specialized pollination systems are an example of this; it is well known that certain orchids would lose the ability for fertilization without their specific bee pollinators (see O'Toole and Raw, 1991). In addition to such specialized systems, it has been shown that bees are essential to the fertilization and reproduction of a large number of flowering plants. The loss of bee diversity will surely be accompanied by the loss in flowering plant species.

Bees as pollinators

Bees may be the most important example of keystone mutualists among the Hymenoptera, as they are absolutely essential to the maintenance of diversity in flowering plants. Studies in the south-western United States have shown that solitary bees are the dominant pollinators of angiosperms in semi-arid areas, that they constitute the most diverse group of flower-visiting insects in these areas, and that a high species diversity in these bees is necessary to maintain high angiosperm diversity (see Neff and Simpson, this volume Chapter 6). Bee feeding requirements and plant pollination requirements are such that a single widespread species, such as the honeybee, cannot effectively pollinate all plants (Torchio, 1990; Neff and Simpson, this volume, Chapter 6; O'Toole, this volume Chapter 7). The loss of bee diversity will surely be accompanied by the loss in flowering plant species. In addition to any environmental repercussions, this could have a much more direct impact as 30% of man's food comes from bee pollinated species (O'Toole, this volume Chapter 7).

Fig wasps as pollinators

Another example of a hymenopterous pollinator is found in the parasitic Hymenoptera in fig wasps (Agaonidae). There are currently about 800 species of fig (Moraceae: *Ficus*) (Mabberley, 1987), most of which are dependent on a single, specific species of agaonid for pollination (Ramirez, 1970, 1974, 1976; Janzen, 1979).

Ant-plant mutualisms

There are a variety of striking examples of interactions between ants and plants, and many plants need their ant associates to survive or propagate (see particularly Beattie, 1985; Hölldobler and Wilson, 1990; Huxley and Cutler, 1991). The usual benefit that plants derive from ants is protection from herbivores, although other benefits include seed dispersal, pollination and supply of nutrients. In exchange for this protection, plants offer ants food and shelter.

Plants provide food for ants in two ways. Extrafloral nectaries are sugar-producing organs that attract animals but do not promote pollination. They are found in a wide range of plants, and are actively utilized by ants. There are many examples of marked increases in herbivore damage to plants bearing extrafloral nectaries when their ant associates are removed (Hölldobler and Wilson, 1990, and references therein). Food bodies are an assortment of epidermal structures, produced by the plant, that can be collected and eaten by ants. They are generally best developed in plant species which also provide domatia for ants, reinforcing the opinion that they are beneficial to ants (Hölldobler and Wilson, 1990, and references therein).

Domatia are structures produced by plants that serve no apparent function aside from sheltering ant colonies. Many forms of domatia are possible, but typical ones are hollow stems, thorns, or expanded leaf bases. Hölldobler and Wilson (1990) present a variety of evidence to indicate that domatia are produced to encourage symbiosis with ants: domatia are almost always occupied by ants in nature; the most complex domatia are typically occupied by only one or a few species of specialist ants; plant species with domatia usually also produce food bodies (which have no known function except to feed ants); domatia are usually inhabited by quite aggressive ant species, often in sharp contrast to timid congeners.

The association between *Azteca* ants and *Cecropia* trees (Cecropiaceae) is one of the best known ant-plant associations in the Neotropics (Longino, 1989, 1991; Davidson and Fisher, 1991, and references therein). *Cecropia* trees have hollow stems which are usually inhabited by ants, and produce food bodies (glycogen) at the petiole bases; the *Azteca* ants vigorously protect the plant against herbivores, especially leafcutting ants. A few species of *Cecropia* do not have these specializations to encourage the *Azteca* ant associates, however these species have waxy stems which are difficult for leafcutting ants to climb (Mabberly, 1987). Schupp (1986) showed that the interaction with *Azteca* ants is directly beneficial to survival of juvenile trees. Young trees grew more vigorously when *Azteca* was present, due to differences in the level of herbivory and vine cover. The *Azteca* not only eliminated most herbivores, they efficiently removed vines from saplings.

The symbiosis between ants and certain *Acacia* species (Fabaceae) is another well known ant-plant association (Janzen, 1966, 1967a, 1969; Hölldobler and Wilson, 1990). The *Acacia* species offer ants food in the form of both extrafloral

nectaries on the stems and food bodies attached to the tips of the leaflets, as well as domatia in the form of enlarged, hollow thorns within which the ants can nest. In return the ants protect the *Acacia* from attack by herbivores, and competition from other plants. Janzen (1966, 1967a, b, 1969) showed that the ant *Pseudomyrmex ferruginea* protected acacias from a variety of herbivores, including membracids, coreids, scarabs, chrysomelids, buprestids, plus various caterpillars. Additionally, they killed any plants sprouting within about 40 cm of ant-occupied acacia trunks. Acacias from which he had experimentally removed ants suffered greatly when compared to nearby ant-occupied plants. During a one-year study, the biomass and growth of unoccupied trees steadily decreased to the point where the ability of the tree to bear seeds, and perhaps even survive, was in question.

Another service ants provide plants is seed dispersal, which is necessary to the continued survival of many plant species. It has been estimated that the seeds of perhaps 35% of all herbaceous plants (as well as many woody species) are dispersed by ants (Beattie, 1985). Myrmecochory (seed dispersal by ants) may increase seedling recruitment by dispersing seedlings over great distances, which eliminates competition with the parental plant and may reduce interspecific competition; and by moving seeds into their underground nests, which can hide the seeds from predators, protect the seeds from ground fires, and promote seedling growth in the nutrient enriched ant nest soils (Hölldobler and Wilson, 1990). The ants benefit from food and perhaps special metabolites, and nest chamber reinforcement. Plants may produce food bodies attached externally to the seed (elaiosomes) which attract ants and encourage them to carry the seeds to their nests.

Ants are clearly important to the survival of many plants (and thus to the maintenance of diversity). As Beattie (1985: 145) pointed out, 'Ant services, either on a continuous basis or as a density response, are crucial to a wide variety of plant species worldwide.' The overwhelming importance of the services ants can provide to plants is demonstrated by the number of separate times plants have evolved some reward to encourage ant associations:

- domatia are known from 90 genera in 36 families of flowering plants and ferns (Hölldobler and Wilson, 1990);
- extrafloral nectaries have been recorded in 98 genera in 39 families of flowering plants and ferns by Bentley (1977), and 68 families of flowering plants by Elias (1983);
- Beattie (1985) and Hölldobler and Wilson (1990) characterized the variation in types of food bodies which evolved in five different plant families;
- myrmecochory occurs in Australia alone in at least 87 genera in 23 families of plants (Hölldobler and Wilson, 1990), and it has been estimated that the seeds of perhaps 35% of all herbaceous plants, and many woody species, are dispersed by ants (Beattie, 1985).

These are not flukes of evolution. The majority of ant-plant mutualisms evolve

as a result of selection on the plant (Beattie, 1985; Hölldobler and Wilson, 1990). The repeated evolution of similar structures through convergence in numerous distinct lineages indicates the ability of ants to alleviate the extreme selective pressure on these plants, and thus promote their survival.

Keystone resource species

Keystone resource species are species which provide some resource critical to the survival of dependent populations. Such a resource might be food, shelter, a nesting site, or the provision of soil suitable for growth.

Ants and soil structure

Ants are one of the major groups of soil turners, and in many areas rival or surpass termites and earthworms (Wilson, 1990). Ants not only turn the soil through their nesting activities, they transport plant and animal remains into the nests which are subsequently mixed with the excavated earth, creating a soil structure rich in carbon, nitrogen and phosphorus. The large earthen nests of *Atta* leafcutter ants in the Neotropics are an example. A single mound can cover up to 600 m² and contain as much as 40 000 kg of excavated earth; the galleries can penetrate 6 m below the surface. *Atta* are the principal agents of deep fertilization in rain forests, where less than 0.1% of nutrients normally penetrate below a depth of 5 cm beneath the soil surface. The enriched soil found in their underground dumps can contain four times the concentration of fine tree roots as in adjacent soils (Haines, 1978; Wilson, 1990).

Ants which provide resources for vertebrates

Ants can also operate as keystone resource species for many vertebrates. In addition to being a food item for certain mammals (such as anteaters, aardvarks, pangolins, etc.), many vertebrates are directly dependent upon ants for other forms of sustenance.

Army ant swarms disturb the arthropod fauna of the soil litter; as these arthropods flee to avoid the ants, they are exposed to, and are preyed upon by, a variety of other species. Some species depend on this food source. Willis and Oniki (1978) list 50 bird species that regularly follow army ants. Most are 'professionals', that is species that get over half of their food, often nearly all of it, from following army ant swarms. Since ants swarm throughout the year, the birds can switch from swarm to swarm with no break in food availability (Willis and Oniki, 1978). Other species of vertebrates also utilize ant swarms, including toads and tineid and iguanid lizards (Willis and Oniki, 1978). Marmoset monkeys also associate with ant swarms (Rylands *et al.*, 1989), principally eating crickets, grasshoppers, cockroaches and spiders which have been disturbed by the ants.

Another resource ants can provide for birds is a protected nest site, and several species of birds are known which nest in ant-occupied trees. For example, in Costa Rican dry forests, the rufous-naped wren (*Campylorhynchus rufinucha*) nests in trees defended by *Pseudomyrmex* species (Young *et al.*, 1990), and in India the white-backed munia (*Lonchura striata*) nests in association with a species of *Crematogaster* (Chattopadhyay, 1980). The rufous woodpecker (*Micropternus brachyurus*) of India and Ceylon actually carves a hole within the side of large nests of a *Crematogaster* species, and lays its eggs within this cavity. The ants run over the nest, eggs and fledglings without harming them, but will attack any other intruder (Skutch, 1977). Bird nests in ant-occupied *Acacia* trees in Central America are more successful in producing fledged young than nests in surrounding trees without ants, presumably due to the ants preventing climbing vertebrate predators from entering the trees (Janzen, 1969; Skutch, 1977). The birds are apparently able to live in the tree without arousing the ants, however snakes or lizards which have been experimentally placed in the trees are promptly repelled by stinging and biting ants (Janzen, 1969; Skutch, 1977).

Keystone dominants

Ant mosaics

Ants influence the arthropod community in which they live in more direct ways. Ant species form mosaics which allow several species of ants to co-exist with dominant and non-dominant status. Dominant ant species not only affect and control the distribution of non-dominant ant species, but also influence both the species composition and abundance of other arthropod taxa. Since, as we have already seen, each species of ant within the mosaic can influence the structure and composition of other plant and animal species, these mosaics appear to be a significant contributory factor to arthropod diversity in the tropics (Gilbert, 1980; Majer, this volume Chapter 5). Ant mosaics, and how they affect diversity, are discussed in further detail by Majer (Chapter 5).

Extinction and Hymenoptera

We are currently entering into a period of mass extinctions which may ultimately rival some of the major extinction spasms in geologic history (for a brief history of extinction see Reid and Miller, 1989: 32–3). Various estimates of present extinction rates are listed in Lugo (1988) and Reid and Miller (1989). Reid and Miller (1989) predicted that extinction rates over the next 25 years may be as high as 15 000–50 000 species per year, or 50–150 species per day (based on estimates of 10 million living species, and a 5–15% rate of extinction over the next quarter century). This equals a rate 1500–5000 times higher than average. Their

figures may be conservative, and estimates of potential extinction rates range as high as 50% by the year 2000 (Lugo, 1988: Table 6.1).

Causes of extinction

The main factor causing the current increase in extinction rates is habitat destruction (through loss, degradation or fragmentation). Other contributing factors are over-exploitation, species introductions, pollution, global warming and cumulative effects of man's interference with the environment (Reid and Miller, 1989). The same forces which result in extinctions can cause a series of other adverse effects which are the precursors to extinction: local species extirpations; loss of genetic diversity within species; and disruption of food webs or communities.

Although habitat destruction is occurring at a global level, tropical environments are being particularly devastated. Erwin (1988) stated that an area of humid tropical forest the size of Honduras is being lost or converted every year. Furthermore, most of the world's diversity is tropical. Myers (1988) stated that tropical forests cover 7% of the earth's surface, yet contain at least 50% of its species; Raven (1988) felt that tropical forests contain at least two-thirds of the world's organisms. Preserving remnants of habitats (in parks or reserves) does not ensure that all habitat species survive. It has been estimated that a 90% reduction in habitat (i.e. preserving a piece of habitat that is one-tenth of the original habitat size) will mean a 50% loss in species (Myers, 1983; Reid and Miller, 1989).

Extinction prone groups

Extinction rates differ among different groups of organisms, with certain groups displaying characteristics that make them more prone to extinction than other groups (Terborgh, 1974; Pimm *et al.*, 1988; Reid and Miller, 1989). Characteristics found in extinction prone groups of organisms include: species at higher trophic levels; local endemics; species with chronically small populations; largest members of a guild; species with poor dispersal and colonization ability; species with colonial nesting habits; migratory species; species dependent on unreliable resources; and species with little evolutionary history with disturbance (Reid and Miller, 1989). While many of these traits seem to apply particularly to vertebrates, others have wide applicability.

Evidence for Hymenoptera as an extinction prone group

Among species of Hymenoptera are many of the characteristics listed above under extinction prone groups. Of particular interest are species at higher trophic levels, local endemics, species with chronically small populations, species with colonial nesting habits and species dependent on unreliable resources. Certain of these traits apply to all Hymenoptera. Unruh and Messing (this volume Chapter

2) point out that, due to genetic considerations, the effective population size in Hymenoptera is less than it would be in other groups having an equal actual population size, thus making the order as a whole more prone to extinctions. However, within the order some groups are more threatened than others.

The obvious exception to Hymenoptera as an extinction prone group are the social Hymenoptera (ants, social wasps, social bees) and these are discussed below. The phytophagous Hymenoptera, in particular the sawflies, also appear to be under no great threat. The groups which appear to be most threatened are the non-social aculeate Hymenoptera and the parasitic Hymenoptera. Species in these groups are at higher trophic levels than their prey, and if they operate in a density dependent manner they can become either species with chronically small populations themselves or species dependent on unreliable resources.

Non-social wasps and bees

Day (1991) listed over 850 aculeate Hymenoptera on Red Data lists, along with an indication of their status as extinct, endangered, vulnerable or rare. Day (1991) did not go into specific reasons for this decline; however, O'Toole (this volume Chapter 7) cites several works documenting the decline of native bees in Europe. Other chapters in this volume present evidence that due to the partitioning of resource and habitat needs for food and nesting sites within a given environment, habitat degradation and destruction can and does result in the decline of populations of aculeate Hymenoptera (Vinson *et al.*, this volume Chapter 3; Gess and Gess, this volume Chapter 4).

Parasitic Hymenoptera

There is little Red Data information for the parasitic Hymenoptera (although see Shaw, 1987); however, evidence that parasitic Hymenoptera are extinction prone has been presented by LaSalle and Gauld (1992), and LaSalle (this volume Chapter 8). Species are at higher trophic levels than their hosts, can have chronically small populations and are often dependent on unreliable resources. The sensitivity of parasitic Hymenoptera has been demonstrated on many occasions in outbreaks of pests that are normally under biological control due to natural or man-made environmental disturbances which cause the elimination of the more sensitive parasitoids but do not eliminate the pest. For a further discussion of extinction and parasitic Hymenoptera, see LaSalle (this volume Chapter 8).

Social Hymenoptera

Wilson (1990) pointed out that no major eusocial clade has ever gone extinct. He stated (1990: 26), 'No group comparable to the termites, ants, and apid bees in social order has gone extinct or even retreated to rare, relict status in isolated parts of the world.' He stated that the larger the population and the less the

numerical fluctuations through time, the longer the waiting time to extinction (Wilson, 1990). While we agree with Wilson that these major clades are in no danger of extinction, species within these clades can be shown to be threatened by displacement by their relatives. Ants as a group might not be going extinct, however numerous species within the group might be endangered. Day (1991) listed almost 100 threatened or extinct species of ants on European Red Data lists.

Consequences of Differential Extinction of Hymenoptera

In a previous section we have discussed keystone species of Hymenoptera. Cascade effect is direct or indirect effect on an ecosystem caused by the removal of keystone species (Reid and Miller, 1989). An example of direct effect would be the ultimate loss through attrition of a plant species due to the loss of its keystone pollinator. The indirect effect could be the loss of all species dependent upon that plant as a keystone resource species.

Cascade effect is not always easy to predict. Gilbert (1980) discussed the importance of 'mobile links' which operate between different food webs in maintaining diversity. He cited euglossine bees (orchid bees) as 'Among the most important and best researched groups of neotropical link organisms' (p.21), and went on to state (p.22) that, 'A single euglossine species may link plant species from all stages and strata of a forest into a system of indirect mutualism'. Thus, the loss of a species of euglossine bee might have unsuspected effects, particularly as the males and females often have different pollination strategies. If the loss of orchid species had a negative impact on euglossine males, the subsequent impact on euglossine females could affect other plant species, perhaps even with adverse economic consequences. For example, euglossine bees are the principal pollinators of Brazil nuts (*Bertholletia excelsa*: Lecythidaceae) (Prance, 1976).

The examples of species reliant on keystone Hymenoptera cited above can all give indications of possible cascade effect which can be caused by habitat degradation. If a species of bee requires dead wood for a nesting site, and dead wood is being removed from forests through fires or gathering for domestic use, then that bee can become endangered or extinct (see Vinson *et al.*, this volume Chapter 3; Gess and Gess, this volume Chapter 4). If that bee is a keystone mutualist necessary to the survival of a plant species, then the plant will become endangered or extinct. If that plant is a keystone resource, then a variety of other species can become endangered or extinct.

The same is true for parasitic Hymenoptera. There are many examples of potentially very destructive pests which are normally held to a minimum level of damage by their hymenopterous parasitoids. The removal of these parasitoids could result in the decline or loss of competing herbivore populations, and in extreme cases the decline or loss of plants. One example of this is the larch sawfly *Pristiphora erichsonii* (Tenthredinidae). This species, which only occasionally

reaches pest status in its native Europe, became a serious forest pest after introduction in North America, and regularly caused losses of 40% of timber volume in Minnesota (Baker, 1972; Gauld *et al.*, 1990). It was partially controlled by a single introduced parasitoid, *Mesoleius tenthredinis* (Ichneumonidae); control failed when the sawfly developed resistance to the parasitoid and became capable of encapsulating and killing the *M. tenthredinis* eggs. A strain of *M. tenthredinis* was found which could overcome the encapsulation reaction of *P. erichsonii*, and the introduction of this strain, as well as a second ichneumonid parasitoid, *Olesicampe benefactor*, have provided improved prospects for the biological control of *P. erichsonii* in North America (Turnock *et al.*, 1976). Other examples of possible cascade effect from the removal of keystone parasitoids are discussed by LaSalle and Gauld (1992) and LaSalle (this volume Chapter 8).

In a specific example of documented cascade effect, it has been suggested that the introduction of the Argentine ant (*Iridomyrmex humilis*) into the fynbos region of South Africa might lead to the extinction of endemic or rare plant species (Bond and Slingsby, 1984). The decline in seedling recruitment in the ant dispersed *Mimetes cucullatus* (Proteaceae) was documented in areas where *Iridomyrmex* has displaced the dominant native ants which displayed various levels of myrmecochory. *Iridomyrmex* differed from the native ants by:

1. being slower to discover seeds;
2. moving seeds shorter distances;
3. failing to store seeds in nests below the soil (and thus leaving them exposed to vertebrate and invertebrate predators and fire damage.

Emergence of *M. cucullatus* seedlings was reduced from 35.3% in areas where *Iridomyrmex* was absent to 0.7% in infested areas; and seedlings were more widely dispersed in areas without *Iridomyrmex*. Bond and Slingsby (1984) suggested that continued invasion of the fynbos by *Iridomyrmex* might result in the eventual extinction of many rare, endemic species of Proteaceae through slow and subtle attrition of seed reserves.

Such displacement of native ant species might diminish the probability of successful reforestation projects in the tropics. Schupp (1986) showed that young *Cecropia* trees have a reduced chance of survival when their *Azteca* ant associates are removed (see above). If habitat destruction enables the displacement of a native ant species during a period when large areas of its plant associate are destroyed, the possibility of ever recovering the native vegetation may be greatly diminished or lost.

We will close with the example of fig wasps as being one of the clearest illustrations of how the loss of a species of Hymenoptera could have devastating effects. Each fig species is dependent upon a specific species of fig wasp for pollination. Solbrig (1991b) cited figs as an example of a keystone resource critical to the survival of primate populations during the dry season. Terborgh (1986: 339) stated, 'All the larger primates use figs heavily, as do procyonids, marsupials, guans, trumpeters, toucans, and many other birds. Figs sustain a high diversity of

species ranging in size from spider monkeys (10 kg) to tanagers (20 g) and constituting up to 60 percent of the frugivore biomass at Cocha Cashu [Peru]. Subtract figs from the ecosystem and one could expect to see it collapse.' Thus, the cascade effect from the loss of a species of fig wasp could be tremendous, yet in their discussions of the importance of figs neither of these authors mentioned the agaonids critical to the survival of individual fig species. When the survival of a keystone resource species is linked to the fate of a partner species, that partner species takes on special importance to the health of the ecosystem.

Conclusions

Arguments for the importance of diversity, as well as justification for the formidable task of attempting to survey and describe the world's biodiversity, have been provided by, among others, Wilson (1985), Reid and Miller (1989), and several chapters in Norton (1986) and Wilson and Peter (1988). Although much of the attention in conservation biology has been focused on vertebrates, more and more emphasis is being placed on the importance of invertebrates and micro-organisms (see Olembo, 1991; and other chapters in Hawksworth, 1991). The reasons for this are apparent: invertebrates and micro-organisms form a large and important component of the planet's biological diversity.

Insects are the major component of this diversity. In terms of species: over half of all living described organisms are insects (Southwood, 1978; Wilson, 1988). In terms of biomass, ants alone outweigh the total land vertebrate population by about 4 to 1 in the Brazilian Amazon and all social insects outweigh the vertebrates by about 7 to 1 (Wilson cited in Holden, 1989). In terms of interactions, food chains comprising green plants, insect herbivores and insect parasitoids contain over half of all known species of metazoans (Price, 1980; Strong *et al.*, 1984; Hawkins and Lawton, 1987). And, as this volume shows, Hymenoptera is a large, important component of insect diversity.

But we are faced with a dilemma: all resources for the study of diversity seem to be dwindling (Edwards, 1984; Wilson, 1985; Wheeler, 1990). Not only do we not have the funds, or the laboratory space, or the museums, or the trained workers – with the current rate of extinctions we do not have the time.

We are presently forced with many difficult decisions concerning how to use our limited resources. Just as scientists have to decide what should be the priority research issues in conservation biology (Soulé and Kohm, 1989; Solbrig, 1991a, b), or what areas or habitats are most deserving of conservation (Vane-Wright *et al.*, 1991; Williams *et al.*, this volume Chapter 14), we also must make difficult decisions as to which groups are most deserving of study. It is imperative that we choose groups for priority study which are the most important for the maintenance of ecological balance and which promote diversity in other organisms.

This chapter is an introduction to the importance of Hymenoptera to biodiversity. Other chapters in this volume present evidence of the importance of

Hymenoptera to ecosystem balance; of the ways in which Hymenoptera contribute to diversity; of the importance of Hymenoptera to agriculture; of the fragility of Hymenoptera in disturbed ecosystems. When choices are made as to which groups merit priority study, Hymenoptera must be one such focal group.

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Intraspecific Biodiversity in Hymenoptera: Implications for Conservation and Biological Control

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Introduction

Populations are challenged by environmental disruption in two ways. First, population size declines because habitat size declines and habitat quality deteriorates. Second, modified habitats change both the intensity and the direction of selective forces which shape population characteristics in future generations. When challenged, populations must adapt or go extinct. Natural selection removes individuals maladapted to prevailing conditions. Adaptation implies that a population both survives a challenge and is able to maintain adequate fitness (including such traits as vigour, fertility and fecundity) and sufficient genetic variation to meet future challenges (Soulé, 1987). Genetic variation for such fitness-related traits is critical for persistence and future adaptation (Schonewald-Cox *et al.*, 1983). Small population sizes and reduced gene exchange among isolated populations result in inbreeding and genetic drift, which are potent forces that reduce genetic variation and erode genetic adaptability and fitness. By extension, genetic variation between populations may determine whether some subset of the populations of a species survive a major environmental challenge.

Other contributors to this volume discuss the crucial role Hymenoptera play in natural and agricultural ecosystems. We supplement those presentations by focusing on selected genetic and biological attributes of the Hymenoptera which

differ from most other insects and which may be cause to reinterpret some views on the distribution and importance of genetic diversity in natural populations. We highlight those aspects of hymenopteran genetic systems which pertain to their sensitivity to inbreeding.

Parasitic Hymenoptera that regulate insect and plant pests in managed ecosystems, especially agriculture, are given special attention. This is appropriate because concepts germane to colonizing and establishing exotic insect populations are similar to those encountered in conservation of endangered populations (Simberloff, 1986). Finally, we address how genetic variation is structured within species and identify cases where intraspecific variation in fitness-related traits have proven important for introductions of parasitic Hymenoptera for classical biological control.

The Hymenopteran Genetic System

Modes of reproduction

Arrhenotoky, the production of males from unfertilized eggs and females from fertilized eggs, is the basic mode of reproduction throughout the Hymenoptera and corresponds to the typical ploidy of the sexes, diploid females and haploid males. Oogenesis in arrhenotokous females is comparable to diploid insects and includes chromosomal recombination and crossing over. Spermiogenesis in haploid males, however, is ameiotic, lacking pairing, recombination and crossing over, although remnants of the first meiotic division are evident in cytological details (Crozier, 1975).

The only other reproductive mode in Hymenoptera is thelytoky; diploid females (and occasionally haploid males) are produced from unfertilized eggs. Thelytoky evolved from arrhenotoky and occurs in significant frequencies in some hymenopteran groups (Crozier, 1975; Stouthamer, 1989). We consider deuterotoky, the parthenogenetic production of both females and males, to be a special case of thelytoky (see Luck *et al.*, 1992). Crozier (1975) reviewed the variety of cytological mechanisms for thelytoky seen in several species. Typically a population is either arrhenotokous or thelytokous with the notable exception of thelytoky and arrhenotoky replacing one another in seasonal cycles in the cynipid gall wasps (Crozier, 1975).

For some populations, the transition from arrhenotoky to thelytoky may have been mediated by microorganisms. Evidence for this proposition comes from experiments where populations of several *Trichogramma* species were permanently transformed from thelytoky to arrhenotoky through antibiotic or heat treatments (Stouthamer *et al.*, 1990a). Microorganisms are now known to mediate thelytoky in three families of parasitic Hymenoptera (Stouthamer, pers. comm.; Unruh, unpublished). Thelytoky has been induced by interspecific hybridizations of arrhenotokous species, again in *Trichogramma* (Nagarkatti,

1970; Pintureau and Babault, 1981). Similarly, thelytoky was transferred from a thelytokous to an arrhenotokous species through mating (Legner, 1987b), although the mechanism for thelytoky in this case is obscure. These examples are reviewed in more detail by Luck *et al.* (1992).

Sex determination

Sex is determined by a balance between autosomal and sex chromosomes in diploid insects. Sex chromosomes *per se* do not occur in Hymenoptera (but see Crozier, 1975), thus chromosomal balance is difficult to invoke. Only one mode of sex determination has been experimentally demonstrated in Hymenoptera: the allelic diversity, or Whiting mechanism (P.W. Whiting, 1943; A.R. Whiting 1961). Sex is determined by a single locus; diploid individuals that are heterozygous become females, diploid individuals that are homozygous or haploid individuals (=hemizygous) become males. Experimental inbreeding has shown that the single locus Whiting scheme obtains in at least eight Hymenoptera species (Luck *et al.*, 1992; Stouthamer *et al.*, 1992): the braconid wasp *Habrobracon hebetor*, the honeybees, *Apis mellifera* and *Apis cerana*, the bumblebee *Bombus atratus*, the stingless bee *Melipona quadrifasciata* and the sawflies *Neodiprion nigroscutem* and *Athalia rosae rificornis* (Naito and Suzuki, 1991) and the ichneumonid wasp *Diadromus pulchellus* (Hedderwick *et al.*, 1988). Cytological or electrophoretic detection of diploid males provides indirect evidence for a Whiting scheme in five ants, *Pseudolasius* sp., *Rhytidoponera* sp. *Solenopsis invicta*, *Lasius* sp., two primitively eusocial bees, *Augochorella striata* and *Lasioglossum zephyrum*, the braconid wasps, *Microplitis croceipes*, and *Bathyplectes curculionis* (reviewed by Stouthamer *et al.*, 1992), and the ichneumonid *Liotryphon caudatus* (Unruh, unpublished). Details for some examples are treated elsewhere (Crozier, 1975; Luck *et al.*, 1992); the implications for biological control are developed qualitatively below and quantitatively by Stouthamer *et al.* (1992).

Because diploid males are non-functional (Crozier, 1975), there is strong selection against their production and, thus, selection for high allelic diversity at the sex locus. The Whiting system is clearly maladapted to an inbreeding lifestyle. A multiple locus model (Crozier, 1975), wherein heterozygosity at one or more of several sex-determining loci yields females, significantly reduces the frequency of diploid males under most levels of inbreeding. However, the inability of strict inbreeding to produce diploid males in other taxa (Skinner and Werren, 1980) is cause to reject allelic diversity as the general plan for sex determination in all Hymenoptera. Alternatives may include dominance and dosage compensation schemes of genic balance but these have not been demonstrated unambiguously in any species (Crozier, 1977; Luck *et al.*, 1992). We return to sex determination and inbreeding in a subsequent section.

Gender allocation and sex ratio

The spermatheca, or sperm storage organ, found in several insect groups, is of special significance in the Hymenoptera because the act of fertilization determines the sex of the zygote. In contrast to most other insects, fertilization is not necessary for the production of a viable zygote (Crozier, 1977). The sex of the progeny is often under female control, assuming she is mated and arrhenotokous. Among other things, control of progeny sex allows females to maximize fitness by adjusting progeny sex ratio to condition of inbreeding and local mate competition (Hamilton, 1967; Green *et al.*, 1982; Werren, 1987). Also eggs of the appropriate sex can be deposited in response to different ecological requirements of the sexes (Charnov, 1982; Werren, 1987).

Gender allocation behaviour is integral to the complex life cycles of some parasitic Hymenoptera and can have important implications for managing endangered populations and colonizing exotic parasitoids for biological control. For example, some Aphelinidae deposit male eggs in one host species and female eggs in another. In these heteronomous parasitoids (Walter, 1983) the availability of both host populations is required for population persistence. In other heteronomous species the male is hyperparasitic on the larvae of its own species (in contrast to attacking a different phytophagous host) while the female remains a primary parasite. In this type, a high host to parasitoid ratio may make encounter of parasitized hosts unlikely. This could reduce male production enough to drive the parasitoid population to extinction. Such constraints on gender allocation have caused biological control introductions to fail (Clausen, 1940) and require special consideration in future introductions (Luck *et al.*, 1993; Stouthamer and Luck, 1991).

Other aspects of sex ratio and gender allocation in Hymenoptera are less easily related to the problems of biodiversity. Progeny sex allocation as it pertains to eusociality (Pamilo, 1991), local mate competition in eusocial species (Hamilton, 1972) and parasitoids (King, 1987; Werren, 1987), and optimal foraging in nonsocial forms (King, 1987; Luck *et al.*, 1993) have recently been reviewed.

Genetic Variation and Population Viability

The concept of minimum viable population size (MVP) (Soulé, 1980) is central to conservation biology. A major assumption of MVP size theories is that stochastic processes are more important than deterministic processes in determining the persistence of small populations. Both demographic and genetic factors contribute to stochasticity (Ewens *et al.*, 1987).

Demographic considerations include both random and environmentally determined variation in birth and death processes. Purely random (environment independent) stochasticity is unlikely to be important until population size falls

below 20 individuals (Gilpin, 1987). Such population bottlenecks may occur at several phases in biological control importations, including initial quarantine colonizations and release into the field (Roush, 1990; Unruh *et al.*, 1983). However, environmental stochasticity, particularly in the form of a catastrophe, is much more likely to determine population persistence than is strictly intrinsic demographic stochasticity (Gilpin, 1987). MVP models incorporating both extrinsic and intrinsic stochasticity have been applied to endangered vertebrate populations (e.g. the spotted owl, the grey wolf and grizzly bear) and the probability of persistence was compared across alternative management practices in various habitats and reserves (see Soulé, 1987 for an overview). To develop similar models for Hymenoptera we need to know more about the fauna so that endangered populations can be identified. Also, we must develop and test demographic models designed around the life history attributes of these insects.

The central theme of genetic MVP models is the reduction in genetic variation and fitness that occurs from reduced population size, inbreeding and genetic drift (Ewens *et al.*, 1987). Inbreeding arises in two ways: first, by a reduction in the number of individuals participating in reproduction (effective population size); second, by intrinsic behaviours that produce mating among relatives (mating systems). Fluctuations in effective population size through time, variation in the sex ratio and variability in reproductive success increase inbreeding in mathematically predictable ways (Lande and Barrowclough, 1987); inbreeding can also be calculated for regular systems of consanguineous mating (Wright, 1951). While environmental stochasticity has a leading place in demographic MVP models, it is seldom incorporated into genetic MVP models (but see Lande and Barrowclough, 1987).

Close inbreeding characterizes the mating systems of many gregarious parasitoids in which females attack isolated hosts. In its extreme, one female lays a clutch of eggs on a host patch and the resulting progeny mate among themselves before leaving the natal site (Hamilton, 1967). This pattern appears to be particularly well developed in Chalcidoidea (Hamilton, 1967, Askew, 1968), some bethyloids (Green *et al.*, 1982) and scelionoids (Waage, 1982), and may also occur in families of ceraphronoids and cynipoids.

Although inbreeding due to reduced population sizes may occur under natural conditions, it is more likely to be a consideration when populations are compressed by habitat modification or during the process of collection and importation of populations for biological control (Mackauer, 1976). Genetic drift is a cumulative process that depends on historical effective population sizes and rates of gene exchange between subpopulations. These can be difficult to measure in nature (Slatkin, 1985).

Genetic MVP models depend on two fundamental premises. First, that quantitative genetic variation for fitness-related traits is ubiquitous in outbred populations and is important for population viability (Lande and Barrowclough, 1987). This must be true if populations are to be capable of genetic adaptation to new conditions (Soulé, 1987). Second, population viability declines under

inbreeding because of the exposure of lethal and sublethal recessive alleles throughout the genome. It is ironic that alleles that are deleterious under present conditions may be those that preadapt a population to future gross environmental challenges (Lande and Barrowclough, 1987).

There are three conceptually distinct types of genetic variation: traditional Mendelian or single locus polymorphisms; quantitative or polygenic traits; and variation in chromosomal structure and number (Lande and Barrowclough, 1987). Karyotypic variation in the Hymenoptera is reviewed by Crozier (1975) and is generally an interspecific phenomenon. Mendelian polymorphisms, such as those detected by electrophoresis, are most often used for monitoring the effects of reduced effective population size and genetic drift on genetic variation (e.g. Unruh *et al.*, 1983). This is unfortunate because evolution and adaptation occur, for the most part, through quantitative changes in polygenic traits rather than by substitutions of discrete effect at single genes (Falconer, 1981; Lande, 1981). Furthermore, quantitative variation is much more resilient to inbreeding or small population size than is Mendelian variation. Heritable phenotypic variation is little affected by modest to high levels of inbreeding. Also, the rate of recovery of quantitative variation is much more rapid than for Mendelian variation following extended inbreeding (Lande and Barrowclough, 1987). Recovery time for neutral single-locus heterozygosity is of the order of a million generations, compared to 100–1000 generations for quantitative traits. Thus, while Mendelian variation is a very sensitive measure of inbreeding in general, it is a poor indicator of current levels of inbreeding because it may reflect genetic bottlenecks in the past and may not accurately reflect current levels of quantitative variation (Slatkin, 1985; Lande and Barrowclough, 1987). (This does not strictly apply when inbreeding is estimated from observed pedigrees.) Hence, Lande and Barrowclough (1987) recommend that both Mendelian and quantitative genetic variation (and chromosomal variation when it occurs) be monitored through time to detect reductions of variation due to small population sizes. A similar approach would provide valuable insights into biological control introductions (Myers and Sabath, 1981; Roush, 1990).

Genetic Variation in Hymenoptera

Single-locus variation

Hymenoptera have roughly one-third the genetic variation seen in diploid insects, using average heterozygosity of electrophoretically detected protein variation as a measure. Average heterozygosity in Hymenoptera is 0.036 versus 0.120 in diploid insects (Graur, 1985). Hypotheses offered to explain this observation include:

1. The niche variation hypothesis (Van Valen, 1965), which suggests that environmental diversity (breadth of the ecological niche) experienced influences

the level of genetic variation maintained. Variation should be less in Hymenoptera because parasitic life habit stabilizes environmental variation during preimaginal development, as does formation of brood cells and temperature control in hives, compared to 'free living' insect forms (Snyder, 1974). Lester and Selander (1979) offer counter-arguments.

2. Effective population size is lower in Hymenoptera because of haplodiploidy in general (Crozier, 1975), because fewer individuals breed in eusocial species (Berkelhamer, 1983; Graur, 1985) and because of inbreeding lifestyles (Hamilton, 1967; Crespi, 1991).

3. Purifying selection removes deleterious alleles exposed in haploid males and genetic loads are reduced (White, 1948; Werren, 1993; but see below and Crozier, 1985, for counter-arguments).

4. The conditions for maintaining a balanced polymorphism are more restrictive under haplodiploid or sex linkage compared to polymorphisms in autosomal diploid systems (reviewed in Crozier, 1985). Also fixation of favourable alleles will occur one-third more rapidly than in autosomal diploid loci (Hartl, 1972).

There have been no definitive tests of these hypotheses (see Crozier, 1985; Graur, 1985; Crespi, 1991, for discussions), however, the observation of little genetic variation in haplodiploid thrips is consistent with the notion that haplodiploidy, through one or more of the above mechanisms, allows less genetic variation than in comparable diploid populations (Crespi, 1991). As Crespi (1991) points out, experimental evaluation of competing hypotheses is needed. For the present all that we can conclude is that Hymenoptera are less genetically variable than most other insect species (but comparable to some other animal groups such as mammals).

Quantitative variation

There have been no comprehensive reviews of quantitative genetic variation in Hymenoptera. Some studies have demonstrated lower phenotypic variation in diploid females compared to haploid males due to the homeostasis arising from diploidy (e.g. Owen, 1989). There is no evidence that quantitative genetic variation is especially low in Hymenoptera, except for those reductions caused by strict inbreeding lifestyles (see below). Among traits that may be valuable for biological control or for populations in modified environments, temperature tolerance, fecundity, sex ratio, gregariousness, dispersal capacity, search rate, handling time, and size are likely to be polygenic (e.g. White *et al.*, 1970; Legner, 1972, 1987a, 1989, 1991; Antolin, 1989). Other attributes such as diapause and host preference are probably coded for by one or a few genes (Bush, 1975; Tauber and Tauber, 1979).

Inbreeding Depression and Genetic Load in Hymenoptera

Inbreeding depression is the term given for the loss of fitness observed in populations when subject to rapid inbreeding. Inbreeding depression is thought to arise from increased expression of recessive deleterious alleles in inbred lineages (Charlesworth and Charlesworth, 1987). A second mechanism, over-dominance, which is fitness superiority owing to heterozygosis, need not be invoked to explain inbreeding depression in most instances (Lewontin, 1974; Lande and Barrowclough, 1987). Inbreeding depression is expected when small populations are founded from large outbreeding ones and subsequently maintained at small population sizes. Such phenomena occur when population sizes are drastically reduced through habitat destruction and may occur when parasitoids are colonized for biological control.

Genetic load is the loss of genetic material through the death or debilitation of some portion of the population which expresses deleterious genes (Kimura and Ohta, 1971). In both diploids and haplodiploids, deleterious genes accumulate by mutation and are purged by selection until a steady state is reached at which loss of deleterious genes counterbalances mutation (Haldane, 1937; Kimura and Ohta, 1971; Crozier, 1985). Thus under the assumptions of constant population size and mutation rate, loss of genetic material (=genetic load) equals the mutation rate. However, when population size declines, or inbreeding increases, the proportion of recessive deleterious genes exposed in homozygous condition increases, increasing genetic load.

Genetic load and inbreeding depression under haplodiploidy

Male haploidy should expose deleterious alleles to 'purifying selection' much more than in diploids (White, 1948), thus reducing the frequency of deleterious alleles. Recently Werren (1993) developed a model which predicts that genetic load is much lower in female haplodiploids and is only slightly higher (or lower) in male haplodiploids compared to diploid species, assuming deleterious alleles are recessive (or partially recessive). Moreover, one would expect chronically inbreeding populations to be less susceptible to inbreeding depression upon enforced inbreeding than normally outbreeding populations because the frequency of deleterious alleles is low from a history of inbreeding (but see Charlesworth and Charlesworth, 1987). Thus, the lower frequency of deleterious alleles predicted for haplodiploids compared to diploids should make the transition from outbreeding to inbreeding significantly easier (Werren, 1993). Hence, many parasitoids and other hymenopteran species that chronically inbreed (see above) may suffer very little from inbreeding depression following genetic bottlenecks arising during biological control introductions or from habitat fragmentation. This should be tested experimentally by estimating genetic load by outcrossing chronically inbreeding species (Charlesworth and Charlesworth, 1987).

A second form of genetic load occurs in hymenopteran species that employ the allelic diversity type of sex determination system; these species suffer the genetic load of non-functional diploid males produced when the sex determining locus is homozygous. The system is comparable to the self-incompatibility systems in plants (Yokoyama and Nei, 1979) and is qualitatively distinct from mutation based loads. The sex determining alleles are effectively recessive lethals in diploid individuals, but unlike typical lethals there are no alternative alleles that are not lethal when homozygous. There is no known sex allele effect in haploid individuals. For a single sex locus system, load equals the inverse of the number of sex alleles segregating, assuming these are at equal frequency, and is minimized when the number of alleles equals effective population size (Yokoyama and Nei, 1979). Estimates of the number of alleles segregating in natural populations range from 5 to 25 (see reference under sex determination), hence, sex determination load varies from 0.2 to 0.04, respectively. This is significantly greater than mutational load which probably ranges from 10^{-4} to 10^{-7} (Kimura and Ohta, 1971; Crozier, 1985; Werren, 1993). Sex determination based loads are even higher when diploid males participate in reproduction and cause the genetic death of their 'female progeny' by producing triploids (Whiting, 1961).

A final attribute of genetic load in arrhenotokous Hymenoptera is the observation of a disproportionate level of female or sex-limited load compared to diploid species (Crozier, 1985, and references therein). Female limited deleterious alleles are not purged by purifying selection in haploid males, thus they will attain a frequency comparable to that in females of diploid species (Werren, 1993). Thus a disproportionate share of the total (female limited, male limited and sex-independent) frequency of deleterious alleles will be female limited (Crozier, 1976, 1985).

The allelic diversity mechanism of sex determination is a critical source of inbreeding depression for those arrhenotokous populations subjected to it. Inbreeding depression will be high under inbreeding and will increase through time if inbreeding continues (Crozier, 1975, 1985; Werren, 1993). In diploid species, and presumably to a lesser extent in haplodiploids, one generation of close inbreeding followed by rapid population expansion results in only slight inbreeding depression (Charlesworth and Charlesworth, 1987; Roush, 1990). However, under the allelic diversity mechanism inbreeding depression will be determined by the number of alleles that survive the genetic bottleneck. In a worst case scenario a female founds a new population by eventually mating with her sons. In this case only two sex determining alleles are segregating and genetic load is 50% (in females) and remains at that level until new alleles enter the population by immigration or mutation. Thus, many populations of Hymenoptera could be easily extirpated by recurrent inbreeding. The extirpation of laboratory populations of parasitoids imported for biological control through sex-determination-based inbreeding depression may be a common phenomenon (Luck *et al.*, 1993; Stouthamer *et al.*, 1992).

A clear research priority should be to determine the taxonomic distribution of inbreeding sensitive and insensitive sex determination mechanisms in the Hymenoptera. The cases known to date show that it is widely distributed among several major taxa but the question remains how common it is within those groups. Similarly, current theoretical estimates of the frequency of deleterious genes in Hymenoptera compared to diploid species should be tested experimentally by measurement of inbreeding depression in laboratory studies (Hoy, 1977; Werren, 1993).

Genetic load under thelytoky

Thelytokous populations are probably composed of a mixture of lineages, each lineage derived from past bouts of recombination (arrhenotoky) or derived by the accrual of different mutations through time. Thelytokous lineages experience no inbreeding when populations suffer bottlenecks but individual lineages will be lost by chance. Loss of lineages can, by chance alone, include the lineage(s) with the lowest level of genetic load in the aggregate population. Thus, through time, the least loaded lineage in the assemblage ratchets up to a more genetically loaded class. This process, called Muller's ratchet, could cause the senescence of parthenogenetic populations (Bell, 1989).

In some cases, thelytokous females retain the ability to utilize sperm and reproduce meiotically (Rössler and DeBach, 1973; Legner, 1987b; Stouthamer, 1989). The genetic recombination that occurs should create new thelytokous lineages with variable levels of genetic load, including some with loads less than their maternal lineage (Bell, 1989; Werren, 1993). Hence populations that sporadically experience bouts of arrhenotoky have reduced load, generally higher fitness, and, by similar logic (Williams, 1975), will be composed of lineages that may cover a greater adaptive spectrum than would strictly thelytokous populations.

One strategy for managing or preserving thelytokous 'species' would be to provide stimuli that promote occasional sexual reproduction. In the case of some parasitic Hymenoptera such stimuli may be removal of endosymbiotic microorganisms which maintain thelytoky (Stouthamer *et al.*, 1990a). Stouthamer (1989) showed that when some thelytokous populations are reverted to arrhenotoky, they have greater fitness (fecundity, and in some cases fertility) than the thelytokous line from which they were derived. This may be evidence of accumulated genetic loads in some of the thelytokous lines that is lost through recombination and selection upon reversion to arrhenotokous reproduction or it is a detrimental effect of the endosymbionts. A possible strategy for biological control introductions may be to induce arrhenotoky, select for desirable traits (and purge accumulated load) and then reinfest the line to yield a thelytokous population with enhanced fitness. Two requirements for this strategy are the ability to reinfest 'cured' individuals with endosymbionts (Stouthamer *et al.*, 1990a) and demonstration that reduced fitness is due to load and not to the endosymbionts themselves.

Outbreeding depression

Dobzhansky (1948) suggested that differential selection and chance may produce 'coadapted genes' that differ among allopatric populations and which optimize fitness for each population's environmental conditions. When populations such as these are hybridized they may display reduced fitness or outbreeding depression (Templeton, 1986). Recent empirical studies of plants (Waser and Price, 1989) show, to the extent that genetic differentiation increases with distance, there may be an optimal outcrossing distance in some species. Outbreeding depression is an important concept for captive breeding programmes of endangered animals where a few individuals from disparate localities may be interbred (Templeton and Read, 1984).

Inbreeding lifestyles in Hymenoptera have been hypothesized to facilitate population differentiation (Askew, 1968). We suggest that these species may be more prone to outbreeding depression or hybrid dysgenesis than outbreeders. Outbreeding depression would be expected, for example, from crosses between populations which differ in karyotype, as seen in a few ants and sawflies (Crozier, 1975). It could also be a problem in biological control programmes when geographic populations of parasitoids or predatory mites (also haplodiploid) are crossed in order to improve their fitness (Force, 1967; Croft, 1970; Legner, 1972, 1987a; Hoy, 1975; but see Messing and Croft, 1991). Outbreeding depression, especially that evinced as unidirectional reproductive incompatibility, is mediated by micro-organisms in some Hymenoptera (Breeuwer and Werren, 1990) and may be more generally applicable than currently thought. Finally, outbreeding may be particularly beneficial for allelic diversity sex determination when a population has few sex determining alleles, such as populations introduced for biological control.

Hymenoptera as Bioindicators of Habitat Fragmentation

Because exact knowledge of biodiversity in any particular ecosystem or community is virtually impossible to obtain, efforts to protect habitats must be guided by monitoring indicator species and using indices in a hierarchical framework (Noss, 1990). Effective population size and the degree and history of inbreeding are two valuable measures of population viability. Herein we argue that sociality, combined with sex determination via the allelic diversity mechanism, may make some Hymenoptera species sensitive indicators of population fragmentation and inbreeding.

Many social Hymenoptera are often restricted to distinct and recognizable microhabitats, and are highly visible members of the community (Hölldobler and Wilson, 1990). Ant nests, wasp colonies and often the large size of these insects make these species relatively easy to census. In ants that show an allelic diversity mechanism of sex determination (e.g. *Solenopsis invicta*, Ross and Fletcher,

1986; *Formica pressilabris*, Pamilo and Rosengren, 1984) estimation of the frequency of diploid drones may provide independent evidence of the degree of inbreeding experienced by isolated populations. For example, *Formica pressilabris* showed diploid males in isolated colonies from marginal habitats but not from centralized colonies (Pamilo and Rosengren, 1984).

Discriminating size differences between diploid and haploid males are known in *Solenopsis invicta*, *Athalia rosae* and *Habrobracon hebetor* (Ross and Fletcher, 1986; Naito and Suzuki, 1991; Grosch, 1945 respectively). Thus, straightforward morphological measurements (or electrophoretic or cytological evaluations) of drones collected during mating flights, coupled with colony census, could provide a simple monitoring procedure that would provide estimates of population size and inbreeding depression arising from habitat fragmentation.

Population Structure

Species are seldom composed of a single population of individuals who mate randomly among themselves. More often species are subdivided into subspecies, geographic races and local populations. Further subdivisions also arise from behavioural attributes of the species. For example, mating systems, nests, colonies and nest aggregations can structure local populations on a finer scale. How genetic variation is organized within the metapopulation or species may provide insight into how to sample populations for biological control introductions. However, there are no simple rules of thumb here because every species or composite of populations falls somewhere on a continuum between one large interbreeding population and virtually isolated subpopulations. Small subpopulations that seldom experience genetic exchange will become highly differentiated by genetic drift (e.g. cave crickets, Caccone and Sbordoni, 1987), while a large interbreeding population of a vagile species will show little or no differentiation throughout its range (e.g. monarch butterfly, Eanes and Koehn, 1978). However, patterns of Mendelian genetic variation within and between subpopulations are greatly influenced by historical phenomena such as past genetic bottlenecks or periodic local extinctions and recolonization (Slatkin, 1985). Hence, inferences about population structure from Mendelian traits, such as enzyme mobility variation, should be treated carefully and not considered a definitive measure of population processes. However, genetic structure produced by mating behaviour is an exciting area of current research.

Allozyme variation has been used extensively to describe mating systems in Hymenoptera, particularly as they pertain to genetic relatedness between altruists and their beneficiaries (Hölldobler and Wilson, 1990 Table 4.1). These studies have benefited from recent refinements of the statistics used to estimate genetic relatedness from electrophoretic data (e.g. Quellar and Goodnight, 1989).

Contrasting genetic variation at the nest level are numerous studies of

genetic (=allozyme) variation among allopatric populations and sibling species complexes in several hymenopteran groups (e.g. ants: Pamilo *et al.*, 1978; Ward, 1980; Halliday, 1981; Crozier *et al.*, 1986; Heinze, 1989; Ross and Trager, 1990; wasps: Metcalf *et al.*, 1984; parasitoids: Unruh *et al.*, 1989; Hung and Schaeffer, 1990; sawflies: Woods and Guttman, 1987). Often little detail is available on biological differences or ecological traits of allopatric populations. Few studies of Hymenoptera (e.g. Ward, 1980) have described the extent of genetic isolation of closely 'allopatric' populations in detail. Nonetheless, unique subpopulations of species, new species and species complexes of Hymenoptera have been uncovered in electrophoretic surveys.

Relevant to biodiversity within species is the relatively common observation of allopatric populations which display diagnostic differences in electrophoretic phenotypes or striking gene frequency differences, e.g. in *Neodiprion* (Woods and Guttman, 1987), *Aphidius* (Unruh *et al.*, 1989), *Formica* (Pamilo *et al.*, 1978). Unfortunately, this differentiation is not necessarily correlated with adaptive trait differences, nor is the converse true. However, molecular differences can provide valuable markers of genetic origin of parasitoid populations imported for biological control. Such markers may be the only indication of which populations became established (e.g. Unruh *et al.*, 1986, 1989).

The Endangered Species Act of the United States and comparable legislation elsewhere seek to protect and preserve biologically distinct entities, while leaving biologists and legal experts to determine how those entities should be characterized (O'Brien and Mayr, 1991). Diagnostic electrophoretic or other biochemical differences are strong evidence that morphologically or otherwise identical populations do not exchange genes and may not have done so for millennia. This may represent scientific justification to protect unique populations. For biological control, evidence of genetic distinctness should justify further efforts to discover biological differentiation (e.g. Unruh and Goeden, 1987). Ultimately biological trait differences between allopatric populations may determine which populations survive environmental perturbation.

Intraspecific Biodiversity as a Resource for Biological Control

Interpopulation variation in fitness-related traits in parasitic Hymenoptera is of proven importance in biological control. Biotype differences (Diehl and Bush, 1984) express themselves both in the probability of successful establishment of parasitoids in selected environments and in the efficacy of pest control. The probability of establishment parallels the general problem of population viability as perceived by the conservation biologist. Table 2.1 lists cases where significant biological differentiation exists among populations of parasitic Hymenoptera. Where multiple biotypes were successfully introduced, trait differences often substantially determined the level of control achieved.

The most widely cited example of the value of biotypes in biological control

Table 2.1. Documented examples of intraspecific variation in life history traits in parasitic Hymenoptera. Most cases were discovered during biological control introductions. When the diversity in traits was beneficial to pest suppression it is noted under 'Control'.

Species (family)	Host insect(s)	Parasite origins	Control ¹	Reference
Temperature Tolerance/Diapause				
<i>Tiphia popillivora</i> (Tiphidae)	Japanese beetle	Three races in Far East	?	Clausen (1978)
<i>Trichogramma dendrolimi</i> (Trichogrammatidae)	Moth eggs	China	?	Caltagirone (1985)
<i>Trioxys comlanatus</i> (Braconidae)	Spotted alfalfa aphid	Italy, Iran	Yes	Flint (1980)
<i>Trioxys pallidus</i> (Braconidae)	Walnut aphid	France, Iran	Yes	van den Bosch et al. (1979)
Host Acceptance/Suitability/Preference				
<i>Aphidius ervi</i> (Braconidae)	Grain aphids	Sympatric Czechoslovakia	?	Stary (1983)
<i>Aphidius thopalosiphi</i> (Braconidae)	Grain aphids	Sympatric Germany	?	Höller (1991)
<i>Aphytis mytilaspidis</i> (Aphelinidae)	Oleander, other scales	Sympatric Greece	?	Rössler and DeBach (1973)
<i>Asobara tabida</i> (Braconidae)	<i>Drosophila</i> spp.	Netherlands, France	—	Mollema (1988)
<i>Aspidiotiphagus citrinus</i> (Encyrtidae)	Red and yellow scales	China, California	?	Flanders (1951)
<i>Bathyplectes curculionis</i> (Ichneumonidae)	Alfalfa weevils	California	?	Caltagirone (1985)
<i>Colpoclypeus florus</i> (Eulophidae)	Summer fruit tortrix	Holland, Italy	?	van Veen et al. (1985)
<i>Comperiella bifasciata</i> (Encyrtidae)	Red and yellow scales	China, Japan	Yes	Clausen (1978)
<i>Comperiella bifasciata</i> (Encyrtidae)	California red scale	Israel, California	?	Blumberg and Luck (1990)
<i>Cotesia glomeratus</i> (Braconidae)	Cabbage white butterfly	Japan	?	Kitano (1978)
<i>Encarsia perniciosi</i> (Aphelinidae)	Red and San Jose scales	Taiwan, Europe	?	Stouthamer and Luck (1991)
<i>Leptopilina bouhardi</i> (Cynipidae)	<i>Drosophila</i> spp.	Europe, Africa	—	Bouletreau (1986)
<i>Mesoleius tenthredinis</i> (Ichneumonidae)	<i>Pristiphora erichsonii</i>	Germany, Canada	Yes	Turnock et al. (1976)

<i>Metaphycus luteolus</i> (Encyrtidae)	Black and soft-brown scales	California, Mexico	?	Clausen (1978)
<i>Muscidofurax raptorellus</i> (Pteromalidae)	Synanthropic flies	Peru, Chile	?	Legner (1987a)
<i>Trioxys pallidus</i> (Braconidae)	Filbert and walnut aphids	Sympatric Europe	Yes	Messing and Allniazee (1988)
<i>Trioxys tenuicaudas</i> (Braconidae)	Filbert aphid	Europe	?	Messing (1986)
Mode of Reproduction				
<i>Aphytis mytilaspidis</i> (Aphelinidae)	Diaspidid scales	Sympatric Greece	?	Rössler and DeBach (1973)
<i>Ceranisus brui</i> (Eulophidae)	Onion and tobacco thrips	Japan, Europe	?	Clausen (1978)
<i>Encarsia perniciosus</i> (Aphelinidae)	Red and San Jose scale	Eurasia	?	Stouthamer and Luck (1991)
<i>Hambletonia pseudococcina</i> (Encyrtidae)	Pineapple mealybug	Brazil, Columbia, Venezuela	—	Callagirone (1985)
<i>Mesochorus nigripes</i> (Ichneumonidae)	Alfalfa weevil	Europe, Colorado	—	Hung <i>et al.</i> (1988)
<i>Technites psyllae</i> (Encyrtidae)	Pear psylla	Switzerland, elsewhere	?	Unruh <i>et al.</i> (1992)
<i>Trichogramma</i> 4 spp. (Trichogrammatidae)	Moth eggs	Sympatric Hawaii, California	—	Stouthamer <i>et al.</i> (1990a, 1990b)

¹(—) indicates academic studies of differentiation, not expressly related to biological control efficacy.

²*Mesochorus nigripes* is hyperparasitic, attacking *Bathypsectes* species which, in turn, attack the alfalfa weevils, *Hypha postica* and *H. brunneipennis*.

is that of *Trioxys pallidus* Halliday, a solitary endoparasitic aphidiid (Braconidae). The introduction of this species into North America is often cited as one of the most successful examples of classical biological control in the world. In fact, it was multiple introductions of distinct 'races' of this species that resulted in substantial control of both the walnut aphid, *Chromaphis juglandicola* Gahan, and the filbert aphid, *Myzocallis coryli* (Goetze), over wide geographic areas of the western United States. Biological control programmes using this species illustrate the adaptive genetic diversity present in both allopatric and sympatric populations relative to three very distinct types of selection pressure:

1. abiotic extremes of temperature and humidity;
2. physiological and phenological suitability of host aphids;
3. lethal chemical toxins, in this case, insecticides.

We use *T. pallidus* to highlight the value of trait differences although several cases in Table 2.1 are comparable. Other types of trait differences evident in the table include differences in the mode of sexuality of biotypes (arrhenotoky versus thelytoky), host selection or preference, and seasonality (diapausing, non-diapausing). Note also that some cases fall into two categories in the table because several traits may vary among populations.

Intraspecific variation in response to abiotic factors

In 1959, in response to increasing levels of damage caused by insecticide-resistant aphids on about 80 000 hectares of walnuts in California, entomologists imported *T. pallidus* from southern France. This French population established readily in the cooler southern coastal counties (van den Bosch *et al.*, 1979), but did not establish in the hotter, drier interior valleys where most of California's walnut production is located, despite frequent and extensive efforts to colonize it there. Subsequently, additional exploration led to the discovery of a population of *T. pallidus* in Iran from areas climatically similar to California's central valley. In 1968 this race was introduced and released. The result was rapid colonization of all major walnut growing areas of the state (van den Bosch *et al.*, 1979), as well as neighbouring Oregon (Messing, 1986). The successful biological control caused by these two ecotypes saved the California walnut growers from 0.5 to 1 million dollars each year, as well as greatly reducing the environmental cost of applying hundreds of thousands of pounds of insecticides in central California (van den Bosch *et al.*, 1979).

Laboratory and field studies of the French and Iranian populations of *T. pallidus* have shown several of the phenotypic differences leading to the biological control observed. The French race of *T. pallidus* has the capability of undergoing aestival diapause in response to hot, dry conditions, while the Iranian race does not (Messinger, 1970). Nevertheless it is the Iranian race that thrives in the hot interior regions of the state, apparently indicating greater heat tolerance by the adults. In a parallel example, two races of the congener *T. complanatus* have

clearly defined differences in climatic adaptation, one of which (Iran) spread throughout the hot areas of California and effectively controlled the spotted alfalfa aphid (Flint, 1980).

This correspondence between native range climate and successful establishment in foreign lands forms the basis for the concept of climatic matching in biological control (Messenger, 1970). Unfortunately, because of our poor knowledge of the biological capacities of most biological control candidates and limited systematic work in many parasitic taxa, application of climatic matching consists of nothing more than matching source and destination climates for foreign exploration, to the extent that it is politically and economically feasible. Also some cases may be discordant with climate relations. An example is the success of two species of *Encarsia* imported from India and Pakistan for the control of the Citrus Blackfly in the southern United States and Mexico. The resulting distributions of these parasites in North America does not neatly correspond to the climates in their native range (DeBach and Rosen, 1991).

In contrast to examples of naturally occurring climatic adaptation, limited attempts to select for altered temperature tolerances in beneficial parasitoids, although successful in the laboratory (White *et al.*, 1970), have never been proven in the field. Temperature tolerance is undoubtedly polygenic in most organisms and there has been no case of successful selection for a quantitative trait that has proven stable and useful for parasitoids in the field.

Intraspecific variation in relation to host suitability

Trioxys pallidus also includes populations using different host aphids. Although Starý (1978) listed *T. pallidus* as a parasitoid of both walnut aphid and filbert aphid in eastern Europe, the populations imported to California and Oregon for walnut aphid control did not parasitize filbert aphid in the field. Subsequently, additional explorations in western Europe resulted in importation of a race of *T. pallidus* which successfully attacked filbert aphid (Messing and AliNiazee, 1989) and led to substantial biological control of this species in Oregon. In laboratory crossing studies it was demonstrated that the two strains were in fact conspecific, producing viable and fertile hybrids, but each strain had significantly different reproductive success on the two aphid hosts (Messing and AliNiazee, 1988).

Intraspecific variation in host suitability has also been observed for the congeneric aphid parasitoid *T. tenuicaudus* (Starý, 1978; Messing, 1986), as well as other parasitoids in the Aphelinidae, Braconidae (Aphidiidae) and Ichneumonidae (see Table 2.1). Bush (1975) presented a model for 'phytophagous parasitic' insects in which new host relationships requiring as few as two gene mutations may lead to sympatric speciation. Askew (1968) provided a similar rationale for rapid genetic divergence among the Chalcidoidea. Haplodiploid reproduction, frequent sib-mating, and discrimination of previously parasitized hosts by adult females all contribute to a high degree of inbreeding that allows small amounts of genetic variation to remain 'fixed' in a population. Thus, potentially valuable

differential host adaptation can be sustained in allopatric (or niche-separated sympatric) populations of a given species. This is a widespread phenomenon among parasitic Hymenoptera and is, thus, profoundly important in biological control.

The mechanisms that underlie host acceptance and host suitability are diverse and may include behavioural non-preference, physiological or nutritional unsuitability, or humoral or immune responses of the host (Vinson and Iwantsch, 1980). In several parasitoid species endosymbiotic micro-organisms may mediate host suitability by overcoming humoral responses (Stoltz, 1986). Thus, at least in some parasitoid–host interactions more than two species are involved and intraspecific diversity may broadly include the genetic diversity of the endosymbionts.

Intraspecific variation in susceptibility to toxins

In bioassays of *T. pallidus* populations from several distinct localities within California, Hoy *et al.* (1991) found significant genetic variation in physiological resistance to organophosphate insecticides. This variation presumably stems from ‘natural’ selection during the 20–30 years since the race was introduced to California. Subsequent laboratory selection has further elevated this resistance (Hoy and Cave, 1991); selected populations were released in the field and persisted in orchards receiving periodic sprays of organophosphates for codling moth control (Hoy *et al.*, 1991). A geographic survey of pesticide resistance/tolerance in the introduced parasitoid *Aphytis melinus* also showed significant variation had developed within a few decades (Rosenheim and Hoy, 1986). Resistance in parasitoids and other natural enemies allows biological control to continue in ‘pesticide-structured’ agroecosystems (Messing and Croft, 1990), where economics dictate continued use of insecticides for other insect pests. In areas of extensive pesticide use, or possibly even in areas with differential exposure to natural toxic compounds, resistant strains of parasitic Hymenoptera may provide valuable biological control in integrated pest management and may be more common than is generally accepted (Roush, 1990).

Conclusions

The genetic system of Hymenoptera, notably haplodiploid arrhenotoky and, in some species, a peculiar method of sex determination, help shape the type and amount of genetic variation their populations contain. These attributes, coupled with distinct biologies, notably in the Parasitica, deserve special consideration when applying general genetic principles in population preservation, management or utilization. In Hymenoptera species where sex is determined by something other than the allelic diversity mechanism, there is probably significant resilience to inbreeding. This is not to say that hybrid vigour will not be observed

in crosses between inbred lines; it does occur (Legner, 1972, 1988) and is a potentially valuable resource in biological control. In species with extreme inbreeding tendencies, inbreeding depression arising from deleterious alleles should not be expected. However, hybrid vigour from over-dominance may be common.

In populations which use the allelic diversity mechanism of sex determination, inbreeding depression can be a severe and sustained problem after a genetic bottleneck. These populations may be especially prone to extinction when they are fragmented or population size is depressed. In other words, this group of Hymenoptera may have a higher minimum viable population (MVP) size than other Hymenoptera or diploid species in general. Because the genetic load arising from this sex determination method can result in the production of non-functional diploid males, it may be relatively simple to monitor inbreeding effects. Thus, certain, easily censused Hymenoptera would be valuable indicator species of habitat disruption. The broad taxonomic distribution of the allelic diversity mechanism for sex determination suggests that it occurs abundantly in several major clades of Hymenoptera (Symphyta, Ichneumonoidea, Formicidae, Apoidea) and a clear research priority for conserving hymenopteran biodiversity should be further elaboration of the distribution of this mechanism.

Additional basic research to clarify the nature of genetic load, the factors mediating parthenogenetic reproduction and numerous other biological and genetic features of the Hymenoptera is needed. The practice of biological control may be the first place where the benefits of such research will be felt. Given that biological control endeavours are, in balance, mediations of man's disruption of natural environments, and they reduce the chemical load in both natural and human settings, then this is a laudable goal. A clear priority for biological control specialists is to measure reaction norms of parasitoid races or allopatric populations and to follow their change after introduction (Myers and Sabath, 1981). In general, theory has far outstripped our biological knowledge of the Hymenoptera, as well as many other taxa. Averting extinctions will be more likely if we have more of this knowledge at our disposal.

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Threats to the Diversity of Solitary Bees in a Neotropical Dry Forest in Central America

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Introduction

Tropical ecosystems are being threatened on a massive scale by man converting the forests to pasture and crop land and by the invasion of these tropical ecosystems by exotic plants and animals. Of these ecosystems the tropical dry forest systems are particularly susceptible to the activities of people because they are easy to access during the dry season with the aid of fire. The rapid loss of tropical dry forests has prompted some governments to set aside some of the remaining dry forests to protect them from being cut. But are these activities enough? Can such forests survive by just being protected from the direct activities of man or are more drastic measures needed?

Our research on the pollination ecology of a dry forest in Costa Rica suggests that such protected forests are under constant threat due to both the activities of people around such forests and the changes brought about by invading species introduced by people into the region. These threats are manifested in many ways and often have a cascade of effects on the various organisms in the forest ecosystem. Our study of the dry season flowering trees and their major pollinators suggest that the survival of many unique aspects of the dry forest may depend on aggressive management of some of the remaining forest resources. But, before any such programmes can be developed an understanding of the diversity of organisms involved in the system, their interrelationships and the importance of these interrelationships to the survival of the system, and the nature of the threats and their effects must be characterized and understood. We will first cover the diversity of the major biological components of the dry season

flowering plant pollinator system and the importance of the behaviour of these organisms to the survival of the pollination system. We will then examine the major threats that presently exist and lastly we will examine the impact that these threats have already had on the system.

Dry Forest Pollination Systems

The lowland Pacific coast of Central America from Panama to Mexico contains a tropical dry forest life zone having a large diversity of plant species. In Costa Rica, about 50% of all flowering plant species in the dry forest are pollinated by bees, and perhaps 40% of this figure are pollinated by large bees, ≥ 1.2 cm in length (Frankie *et al.*, 1983). The remaining flowering plants are pollinated by moths, bats, flies, wasps and beetles (Baker, 1973; Frankie, 1975; Gilbert, 1975; Heithaus *et al.*, 1975; Heithaus, 1979a,b,c; Haber and Frankie, 1989).

Most of the large bee-pollinated plants are trees or vine/lianas, which bloom in the long dry season. The majority of these trees and climbers produce massive displays of colourful flowers. The flowers last only a day and are replaced over several days on each tree. Most are hermaphroditic; and almost all are self-incompatible (Bawa, 1974). Many of the flowers produce nectar (Bolten *et al.*, 1979; Baker and Baker, 1983; Frankie and Haber, 1983; Frankie *et al.*, 1983; Hartshorn, 1983). A lower percentage produce a pollen reward, and very few species produce oil instead of nectar (Frankie *et al.*, 1983).

Diversity of flowering trees and their pollinator needs

The massively flowering, nectar-producing trees are pollinated by a group of relatively large, solitary bees in the genera *Centris*, *Epicharis*, *Xylocopa* and *Gaesischia* (Anthophoridae); and to a lesser extent *Euglossa* and *Eulaema* (Apidae). These large bee pollinators are important to the outcrossing success of the large nectar resource trees, but there are other forest resources important to these bees, particularly the *Centris* on which we will concentrate in this discussion. One of these resources is pollen, which is needed by all bees. *Centris* bees also require oil-producing plants for successful nest provisioning, this resource being represented in the dry forest by the Malpighiaceae. Thus, the bees are dependent on several different sources for their nutritional needs and reproductive success, as are the trees they service. However, bees also require additional non-nutritional resources and environmental conditions for successful reproduction. These resources include sites where male bees maintain and defend territories necessary for mating success and dead wood for building nests. However, the dead wood must contain holes produced by wood boring insects. These interrelationships are shown in Fig. 3.1. We focus our attention on the Lomas Barbudal Biological Reserve and the surrounding Tempisque region of Guanacaste Province, Costa Rica.

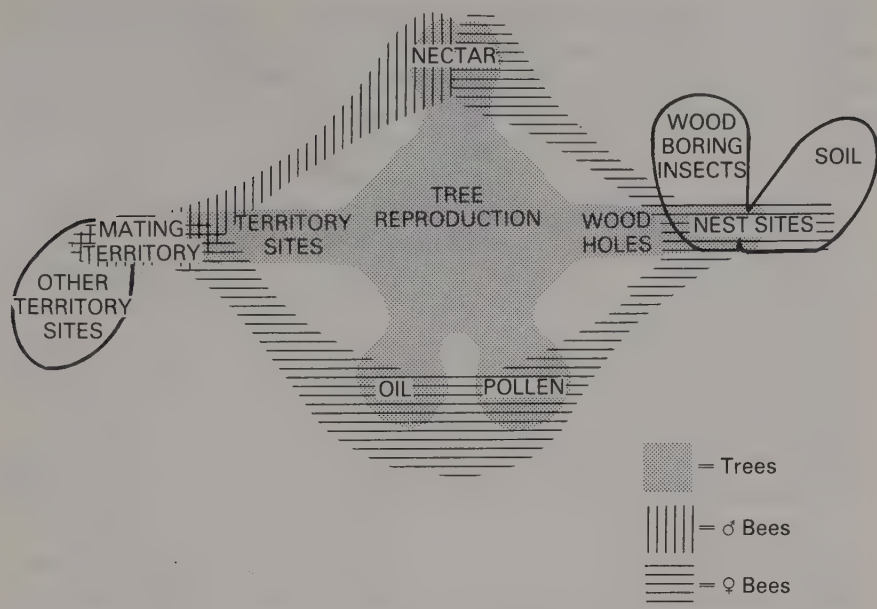


Fig. 3.1. A diagrammatic representation of the interrelationships of male and female *Centris* with several different attributes of forest trees and other select factors. Different trees supply nectar, pollen, oil, sites for mating territories and nest sites. Some nest sites involve wood boring insects of trees, some also need access to soil; others nest in the ground. Mating territories can occur in trees or other sites.

The bees (pollinators) and their resource needs

Of the approximate 250 species of bees that occur in the Tempisque dry forest region of Costa Rica, there are six sympatric species of xylocopids and 14 species of *Centris*. The *Centris* species, which are the main focus here, are listed in Table 3.1. Each has a different set of environmental conditions and resources required for nesting, and the successful reproductive behaviour of males is dependent upon other conditions and resources. We will first examine male territoriality and then nesting requirements.

MALE TERRITORIALITY

The males of each of the 14 species have been observed to initiate, defend and display within a territory, each of which is unique in: (i) the size of the territory defended; (ii) the plant or plants associated with the territory; (iii) the source and chemical nature of secretions used by the males in defining their territory and presumably in attracting females; (iv) the frequency of marking; and (v) the daily territorial period. Details of the territorial activity of some of the species are

Table 3.1. The subgenera and species of *Centris* common to occasional species of *Centris* in and around the Lomas Barbudal Biological Reserve and other selected sites¹ (see Snelling, 1984, for a taxonomic treatment of *Centris*).

(<i>Centris</i>)	(<i>Tachina</i>)
<i>C. adanae</i>	<i>C. fuscata</i>
<i>C. aethyctera</i>	<i>C. heithausi</i>
<i>C. flavifrons</i>	(<i>Hemisiella</i>)
<i>C. flavofasciata</i> ¹	<i>C. nitida</i>
<i>C. aethiocesta</i> ¹	<i>C. trigonoides</i>
<i>C. inermis</i> (= <i>segregata</i>)	<i>C. vittata</i>
(<i>Heterocentris</i>)	(<i>Xanthemis</i>)
<i>C. analis</i>	<i>C. lutea</i>
<i>C. bicornuta</i>	

¹ Most common on the Pacific coast beach strand, Tempisque region.

provided by Frankie *et al.* (1989) and Coville *et al.* (1986). However, three species, *C. adanae*, *C. aethyctera* and *C. nitida*, which differ in several characteristics of their territorial display, are discussed here to demonstrate how their territorial behaviour affects the reproductive biology of large bee-pollinated trees. These three species also demonstrate the diversity of requirements needed by male *Centris*. Territories of *C. adanae* are established by 0800 h Central Standard Time (CST), in openings or patches in the grass of the savannah. These patches are about one or two metres in diameter consisting of bare soil, short grass, or short weeds surrounded by tall grass (Frankie *et al.*, 1980). During the maintenance of a territory a male either perches on a small object near the centre or hovers near the centre of the patch, changing from hovering to perching several times during a minute. Every few minutes the male flies to grass upwind of the patch and marks the blade or stem using glands opening through its mandibles. Generally the marked area covers 2–5 cm of stem or blade length which is coated with a mixture of terpene alcohols, terpene esters and fatty acid esters produced in the mandibular gland of this species (Vinson *et al.*, 1982). The floral odour of these volatile secretions resembling the odour of citronella can often be detected by humans 4 or 5 m downwind. As the time passes, the frequency of marking decreases.

The male constantly defends his territory and when other insects fly into or near the territory the resident male will chase them for 2–3 m. In contrast males will chase conspecific males 10 m or more. All of these activities would be expected to require considerable energy and this is reflected in the decrease in the nectar present in the crop of males during their territorial display (Table 3.2). By 1100 h CST the amount of nectar in the crop is nearly depleted and this coincides with the end of the daily territorial period of *C. adanae* (Frankie *et al.*, 1980). By 1500 h CST sleeping aggregations of males develop (Frankie *et al.*, 1980) and

males collected from such aggregations the following morning have a crop full of nectar. The period between 1130 and 1400 h CST coincides with an increase in bee activity on many nectar producing trees (Frankie and Haber, 1983). This increase in bee activity on the major flowering nectar sources is due primarily to male *Centris* which are one of the major pollinators of these nectar producing, dry season flowering trees (Frankie *et al.*, 1976).

The male territoriality of *C. nitida* is similar to *C. adanae* in that they mark the surrounding upwind vegetation during their territorial display. However, *C. nitida* secretes ketones (musky odour to some people) produced and released from glands located in the femur and tibia of the hind legs (Williams *et al.*, 1984) rather than mandibular glands, which in this species are very small (Vinson *et al.*, 1984). The territories defended by *C. nitida* are located in large trees such as *Byrsonima crassifolia* and *Cassia grandis*. The activity of chasing other bees and conspecifics during their territorial period (from 0800 to about 1300 h CST) may play a role in reproductive outcrossing of flowering trees, although flowering is not a requirement for these territories. In fact, most of the *Centris* species prefer to defend territories in one or two specific tree species regardless of the flowering condition (Frankie *et al.*, 1989).

Both *B. crassifolia* and *C. grandis* trees in which *C. nitida* defends territories are sites also preferred as territorial sites by *C. flavifrons* and *C. inermis* (Frankie *et al.*, 1989). However, interspecific overlap of territories rarely occurs. For example, *C. flavifrons*, one of the larger species, prefers to defend territories near the tops of trees generally in hollows framed by the twigs and leaves. The medium sized *C. inermis* tends to defend territories downwind of branches in the lower crown, a site also preferred by *C. nitida*, the smaller of the three. However, *C. inermis* has not been observed to maintain a territory in the same individual tree as *C. flavifrons* or *C. nitida*. Although smaller, *C. nitida* was observed to replace *C. inermis* from a *C. grandis* tree (Frankie *et al.*, 1989), and such replacement did not appear to involve physical attack but was possibly due to more powerful volatiles or volatiles that are not compatible with those of *C. inermis*.

Table 3.2. The nectar reserves of male *Centris adanae* at various times before and during the maintenance of their territories (adapted from Frankie *et al.*, 1980).

Activity (time in territory)	No. bees sampled	Average nectar in crop (μ l)
Morning sleeping aggregation	5	39.8
Marked 25+ times in territory (20 min)	3	28.4
Marked 120+ times in territory (120 min)	3	10.3
Marked 160+ times in territory (180 min)	4	2.3

Several cases are known where the blend of compounds determines the attraction or repellency of a pheromone mixture (Tamaki, 1985). Such a suggestion merits further study but also suggests that the territorial sites utilized by these three species are restricted to a select group of trees which are limited in number and not effectively shared.

Male *Centris aethyctera* are similar to the other species in that they defend territories, but in this species the territories are large (8–9 m across) and are generally located 0.5 to 1 m downwind of small to medium sized trees, rather than in the tree hollows. The territory of this species differs from the others in two additional respects. One is a lack of marking (Frankie *et al.*, 1989) which is consistent with the lack of evidence of glands for such a purpose (S.B. Vinson, unpublished). The second is a preference for several flowering tree species rather than a particular tree species. In fact, *C. aethyctera* has been recorded to defend territories on 10 species of nectar or pollen producing trees when in flower. Because of their territorial preference for flowering trees, the wide group of tree species in which they defend territories, and the large area of a tree they patrol, *C. aethyctera* may be particularly important in repelling bees, an act which would be expected to increase outcrossing.

FEMALE NESTING

Females nest in a variety of substrates where from one to several cells are constructed and provisioned with oil and pollen. The excavation of nests in the earth is probably primitive as this is the situation found in many subgenera and related genera (Vesey-FitzGerald, 1939; Roubik and Michener, 1980; Coville *et al.*, 1983). Species of the subgenera *Hemisiella*, *Heterocentris*, and *Xanthemisia* have adapted to use existing holes as nest sites, often in dead wood. The nest site preferences for the 14 species nesting in the dry forest of Costa Rica are provided in Table 3.3 along with two more species that are more common in sandy areas such as beach strand. Although six species use existing holes in dead wood, each has a specific requirement in regard to hole diameter, location within habitats and materials needed for nest construction (Frankie *et al.*, 1989). The number of cells per nest is also generally characteristic of each species. Ground nesting species such as *C. adanae*, *C. flavifrons*, *C. flavofasciata* and *C. aethiocesta* usually only produce and provision one cell per nest. In contrast *C. aethyctera*, another ground nester, produces four to six cells in each nest (Vinson and Frankie, 1977). The cells are constructed of a resinous, waxy-like material of unknown origin in which soil or wood chips are embedded. The cells are provisioned with pollen from several trees (Fig. 3.2) and oil primarily from *B. crassifolia* (Frankie *et al.*, 1983; Vinson, Williams, Frankie, Rojas, in prep.). Thus, female *Centris* are particularly important pollinators of these pollen and oil producing plants. Although females forage for nectar presumably for maintenance, they may be less important in pollinating nectar plants than males which appear to have higher energy demands.

There are other resources and conditions needed for nesting by *Centris*. Tree

Table 3.3. Preferred nesting habitats and substrates used by 14 species of *Centris* found in the Costa Rican dry forest (Tempisque region).

Species	Preferred nesting habitats ¹	Nesting substrate ²
<i>C. adanae</i>	Forest and savannah	Soil
<i>C. aethyctera</i>	Savannah	Soil
<i>C. flavifrons</i>	Savannah	Soil
<i>C. flavofasciata</i> ^{3/}	Beach-exposed	Sand
<i>C. aethiocesta</i> ^{3/}	Beach-shaded	Sand
<i>C. inermis</i>	Forest	Soil
<i>C. fuscata</i>	Forest	Soil
<i>C. heithausi</i>	Forest	Soil
<i>C. analis</i>	Forest	Wood & W
<i>C. bicornuta</i>	Forest	Wood & W
<i>C. nitida</i>	Forest	Wood & S
<i>C. trigonoides</i>	Forest	Wood & S
<i>C. vittata</i>	Forest	Wood & S
<i>C. lutea</i> ^{4/}	Savannah	Wood & W

¹See Frankie *et al.*, 1988; Frankie *et al.*, submitted.

²W = wooden holes lined with wood chips; S = wooden holes lined with soil.

³Found primarily in beach sand.

⁴Only one nest discovered.

hole nesting species require dead wood with the proper diameter holes (Frankie *et al.*, 1988a). Females modify the tree holes with the addition of either soil or wood chips to provide a tube of uniform diameter in which cells are placed. These same materials are used between cells, as well as being mixed with the resinous, waxy material to form the cell that will be provisioned. But the soil particles and wood chips may not be in ready supply. For example, the soil and wood chips are generally fairly uniform in size ranging from 0.1 to 0.8 mm. In the case of soil, four different collecting sites have been found. These sites have been located near rivers in deep, shaded forest; in two cases on the edge of a path in the forest floor made by the repeated passage of an animal, in one case the site involved soil from an uprooted tree, and in the other case soil brought up by a burrowing lizard. Each site was characterized by fine soil with a very shallow pit free of debris about 14–18 cm across (Fig. 3.3A). Such sites may be limited. This is suggested from observations on one such site where three species (*C. nitida*, *C. trigonoides* and *C. vittata*) were recorded collecting soil and in several moments as many as three bees of the same species were present. Females would stand in the pit, bury their hind legs into the soil which would stick to their corbicula (Fig. 3.3A), and after withdrawing their legs they would fly to the nest (Fig. 3.3B). A source of wood chips may also be limited since the bees do not excavate the holes themselves and many wood boring insects either do not

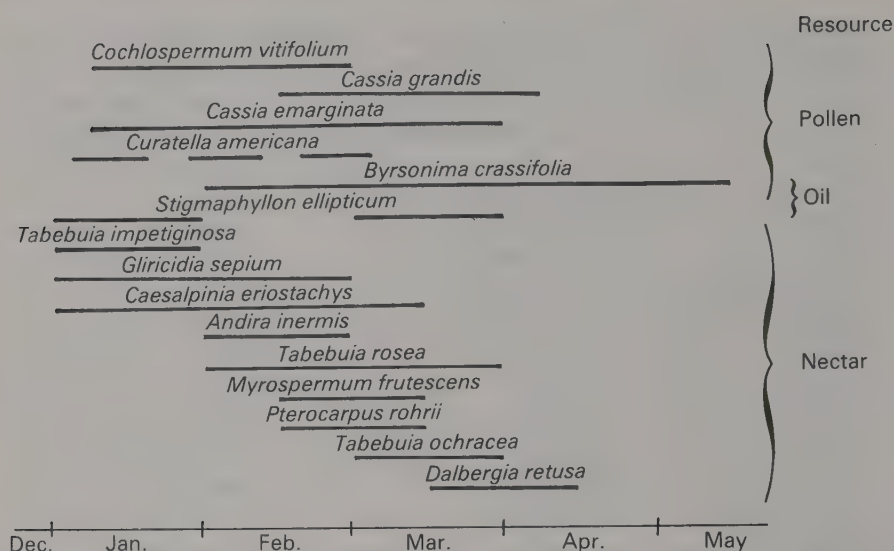


Fig.3.2. Flowering period of the more important resource trees for *Centris* in the dry forest of Costa Rica. For additional species and detail see Frankie *et al.* (1983).

produce sawdust or the sawdust is readily scattered by the constant wind that occurs during the dry season. Bees collected after having collected soil or wood chips revealed that in some cases oil and in others water was used to stick the soil or wood chips to their hind leg.

Not all dead wood with proper hole diameter is suitable for nests. We have indirect evidence that wood exposed to the intense sun (i.e. not shaded in dense forest canopy), gets too hot for bee development (Frankie *et al.*, 1988a). But the wood nesting bees are not the only ones that have specific requirements. Ground nesting species such as *C. adanae* and *C. flavifrons* nest in moist, sandy loam just below the surface and appear to require soils at least 5–10 cm deep as we have not located nests in similar soils 2–3 cm deep near by. In contrast, *C. aethyctera* nests in a variety of habitats ranging from thinly covered, rocky soil to sand (Vinson and Frankie, 1991). Both *C. flavofasciata* and *C. aethiocesta* have been reported only from sandy soils (Snelling, 1984; Vinson *et al.*, 1987; Vinson and Frankie, 1988).

The trees, the diversity of resources offered and their service needs

In the dry forest of Lomas Barbudal there are four seasonal tree flowering patterns that can be recognized (Frankie *et al.*, 1974a,b). Two occur during the dry season (Fig. 3.4), which begins in January and continues through April during which over 30 large bee pollinated tree species flower. Each has a distinct and specific flowering period (Frankie *et al.*, 1983), some flowering over several

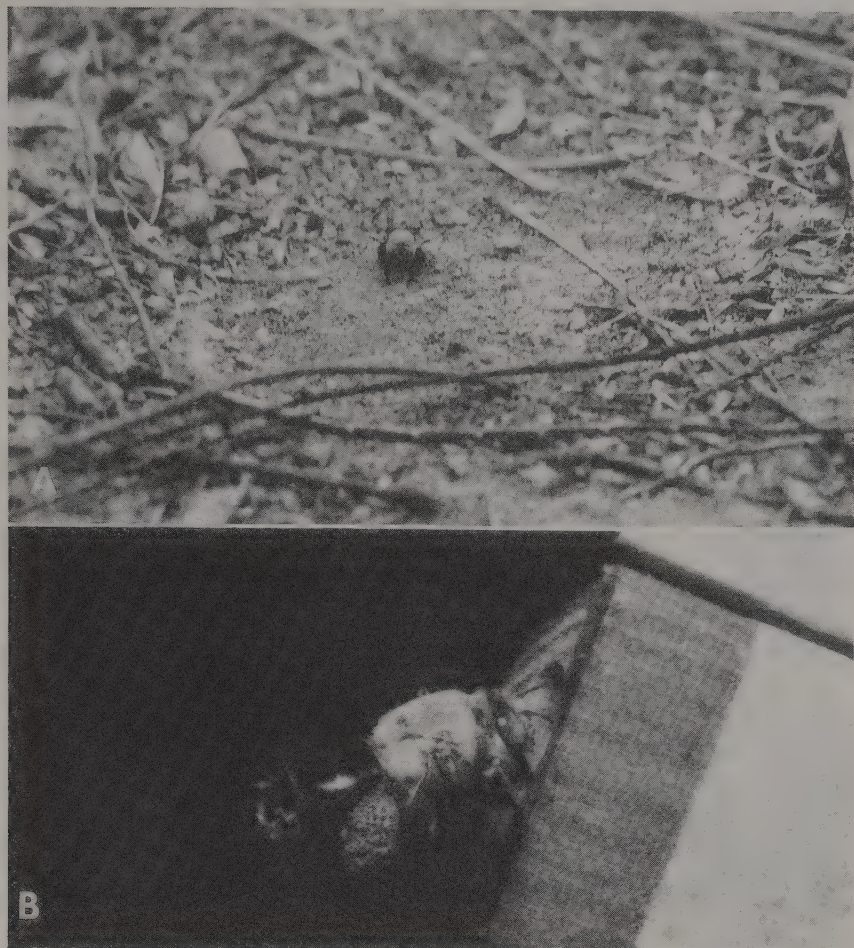


Fig. 3.3. (A) *Centris nitida* female collecting soil from a soil collecting area in the forest floor. (B) Female *C. nitida* showing soil on the hind legs as she enters a wooden nest block.

months while others only flower over a two-week period (Fig. 3.2 above). Baker (1973) discussed the possible evolutionary importance of the existence of an unbroken sequence of flowering that provides a continual resource base for the pollinators. For *Centris* bees this unbroken availability may extend to three different types of flower resources (Fig. 3.2 above), nectar, pollen and oil, each produced by a different set of trees. Table 3.4 lists the dominant trees or vines utilized by *Centris* bees in Lomas Barbudal, and Fig. 3.2 shows flowering period and type of resource produced by several of these species.

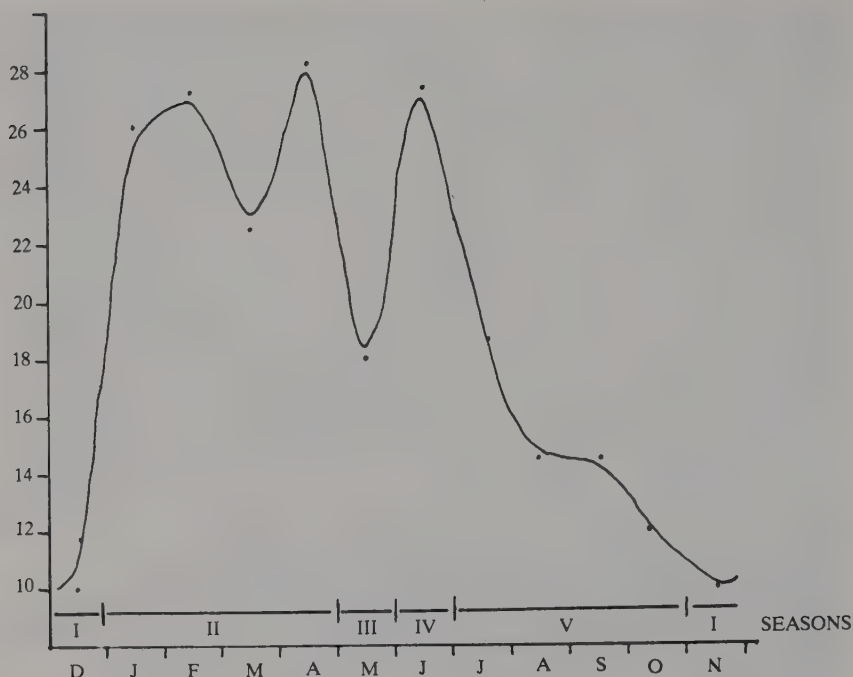


Fig. 3.4 Number of flowering trees in the Costa Rican dry forest at various periods during the year. Four different flowering periods can be seen, two of which occur during the dry season (II). I = wet/dry season transition, II = mid-dry season, III = late dry season, IV = dry/wet season transition, V = wet season (after Frankie, 1975).

NECTAR RESOURCES

Although there had been speculation as to whether the widely spaced, con-specific plants in the lowland dry forests were self- or cross-pollinated (Corner, 1954; Baker, 1959; Ashton, 1969), there is presently considerable evidence that these plants are regularly cross-pollinated (Bawa, 1974; Frankie *et al.*, 1976, 1983; Frankie and Haber, 1983). The importance of interplant movement by bees of one kilometre distances was emphasized by Janzen (1967, 1971) and Janzen *et al.* (1982) who examined the potential importance of long distance movement of euglossine bees in pollination and suggested similar roles for some of the other large bee species of *Centris*, *Xylocopa*, *Ptiloglossa* and *Bombus*. It has now been established that these bees constitute the major pollinators of many of the tree species in these forests (Frankie, 1975, 1976; Frankie *et al.*, 1976, 1983). This is particularly true for the nectar producing trees and the importance of these large bees was further emphasized by Frankie *et al.* (1976), who reported

Table 3.4. Some important tree and vine species utilized by *Centris* bees in Lomas Barbudal. Nomenclature for the tree species follows Hartshorn and Poveda (1983) while the vine species follow Janzen and Liesner (1980) except that the Caesalpinioideae is placed here as a subfamily of the Fabaceae according to that used by Wiersema *et al.* (1990).

Bignoniaceae

- Godmania aesculifolia* (HBK) Standl.
- Tabebuia impetiginosa* (Mart. ex DC.) Standl.
- Tabebuia rosea* (Vertol.) DC.
- Tabebuia ochracea* (Cham.) Standl.

Cochlospermaceae

- Cochlospermum vitifolium* (Willd.) Spreng.

Dilleniaceae

- Curatella americana* L.

Fabaceae (=Leguminosae)

Caesalpinioideae

- Caesalpinia eriostachys* Benth.
- Cassia biflora* L.
- Cassia emarginata* L.
- Cassia grandis* Lf.

Faboideae (=Papilionoideae)

- Andira inermis* (Swartz) HBK
- Dalbergia retusa* Hemsl.
- Gliricidia sepium* (Jacq.) Steud.
- Myrospermum frutescens* Jacq.
- Pterocarpus rohrii* Vahl.

Malpighiaceae

- Byrsonima crassifolia* (L.) DC
 - Hiraea reclinata* Jacq.
 - Stigmaphyllon ellipticum* (HBK) Adr. Juss.
 - Stigmaphyllon lindenianum* Adr. Juss.
-

that the leguminous tree *Andira inermis* was self-incompatible, thus requiring effective outcrossing mechanisms.

But, *A. inermis* is a massive flowering tree with abundant resources so what factors ensure this outcrossing? Although the flowering period is generally described as synchronous (Opler *et al.*, 1980), there is variability in both the quantity and timing of nectar production (Frankie and Haber, 1983). For example, the flowers of *A. inermis* open between 0730 and 0830h CST and yield an average of 0.8 μ l nectar, this flow drops but begins to flow again between 1100 and 1400h CST averaging 1.6 μ l per flower, flowers only functioning

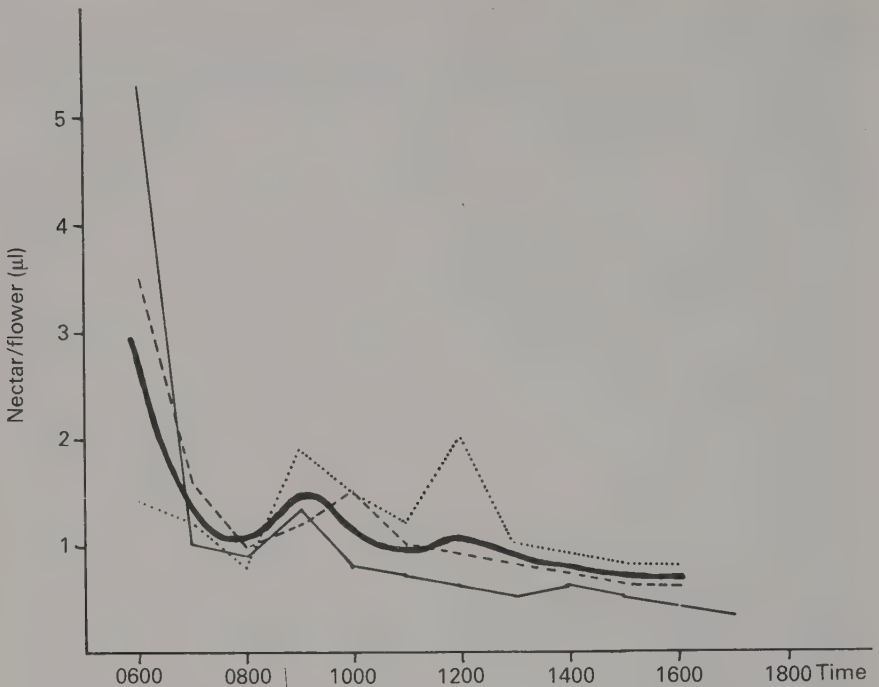


Fig. 3.5. The production of nectar over time for *Caesalpinia eriostachys* (after Frankie and Haber, 1983). The solid heavy line is the average of three different trees.

for one day. Bimodal nectar peaks have also been found for temperate plants (Carpenter, 1976; Frankie and Vinson, 1977; Brown *et al.*, 1981).

In addition to bimodal nectar production, there is also variability in production between trees. For example, three different *Caesalpinia eriostachys* trees had three different nectar flows (Frankie and Haber, 1983) resulting in a general pattern in the nectar flow (thick line, Fig. 3.5) made up of a variation in specific patterns. But there is also a difference in pattern on the same tree through time. Again, an example can be taken from the Costa Rican dry forest where Frankie and Haber (1983) reported that the nectar flow of *Myrospermum frutescens* differed on the same plant over three days within a week. There is also variability in the composition of nectar from one individual tree to another. For example, Frankie *et al.* (1982) found differences in sugar concentration and composition of the nectar of *Tabebuia rosea* in Costa Rica. The result is a great variability in the temporal and spatial presentation of nectar resources. This may be extremely important because it prevents the bees from keying on a particular plant at a particular time. The bee must sample several trees to find adequate rewards and moving to conspecifics offers the possibility of better rewards. The importance of

this can be further emphasized because of the propensity of Hymenoptera to learn (Alloway, 1972; Vet, 1988), which is reduced by the great diversity in the nectar flow. But this also points out the importance of plant diversity in maintaining the health of the system. While such variation in resource patterns may increase the movement of bees and pollen between trees, other facts may also play a role.

A second factor may be the large number of bee species and individuals visiting the resource. Frankie *et al.* (1976) reported 70 species of bees visiting *A. inermis* with peak periods at anthesis (about 0730h CST) and during the second nectar flow which occurred around noon CST. The large number of bees rapidly reduced the resource, thus causing other bee species to seek other resources which likely include other conspecific trees (Thorp, 1969; Free, 1970; Frankie and Baker, 1974). However, two other factors have also played a role in the dry forest of Costa Rica. One is group bee foraging and the second is male territoriality.

Group foraging was described by Frankie and Baker (1974) and was reported for three species of anthrophorid bees, *Gaesischia exul*, *Centris aethyctera* and *C. adanae*. These bees were reported in aggregations consisting of as few as 10 to over 300 bees, generally all conspecifics (primary males) clustered in a space of 0.5 to 2m as they forage through a tree. As suggested by Frankie and Baker (1974), as these foraging aggregations move through the tree, the numerous interactions, nectar removal and buzzing noise may chase off other bee species from the tree to forage on other conspecific trees near by.

Male bee territoriality is not only important to the reproductive success of the bees (discussed above), but it may be another factor influencing outcrossing. Although several authors (Stiles and Wolf, 1970; Linhart, 1973; Stiles, 1975) suggest that territoriality may restrict pollen flow, their suggestion is based on resource defensive behaviour. However, male *Centris* territories are often not associated with resources, but instead they maintain and defend territories in which they release factors to attract females (Frankie *et al.*, 1980; Vinson *et al.*, 1982; Vinson and Frankie, 1990). These types of territories are known as leks (Alcock, 1980, 1987). During the territorial period (generally from sunrise to midday) these aggressive males chase intruders many metres from their territory (Raw, 1929; Rozen, 1958; Stephen *et al.*, 1969; Thorp, 1969; Rozen, 1970). When these territories occur in a flowering tree, which is often the case for *C. aethyctera*, they may repel foragers which then move to conspecific trees.

POLLEN RESOURCES

In addition to trees producing nectar, there are trees that are important in the production of pollen which is a resource also needed by bees. The large tree *Cochlospermum vitifolium* is primarily a pollen producer with synchronous, rapidly opening (between 0500 and 0600h CST) flowers that last one day. *Cassia grandis* L. is also primarily a pollen producer having synchronous and rapidly opening flowers that open around 0500h CST (Frankie *et al.*, 1983).

Other common pollen sources for *Centris* include *Cassia biflora*, *Cassia emarginata*, *Byrsonima crassifolia* and *Curatella americana*. As seen in Fig. 3.2 above, these different pollen resource species also flower during specific times during the dry season. Unlike many of the large bee pollinated nectar producing trees, the pollinators of these trees are the females of several species of *Centris* and *Xylocopa*. However, *Centris* prefer trees to shrubs, thus *C. biflora* is probably a less important pollen source for this group (Frankie and Coville, 1979).

Several of these pollen resources also serve as territorial sites for several *Centris* species and it is among these pollen resource trees that male territoriality may be particularly important. Large *C. grandis* trees often have territories of male *C. aethyctera*, *C. vittata*, *C. nitida*, or *C. heithausi* while *C. vitifolium* trees support territories of *C. fuscata* or *C. aethyctera* (Frankie *et al.*, 1989). The males of all these species except *C. nitida* never or rarely mark and may exhibit a resource territorial defence (Alcock, 1980). They also defend their territories against other bee species and may cause females to leave the tree canopy only after collecting pollen from a few flowers due to the disturbance caused by the territorial male (Frankie and Baker, 1974).

OIL RESOURCES

The third group of plants consists of members of the Malpighiaceae which are important primarily to *Centris*, which are known as oil collecting bees (Vogel, 1969; Neff and Simpson, 1981). In the Costa Rican dry forest the 14 species of *Centris* all appear to be dependent on these oil producing plants, primarily *B. crassifolia*. Although most are vines, *B. crassifolia* is a large tree with an extended flowering period, on which female bees gather both oil (Buchmann, 1987) and pollen. The common oil producing vines include *Stigmaphyllon ellipticum*, *S. lindenianum* and *Hiraea reclinata*, but only *S. ellipticum* (Fig. 3.2) may be significant since the other two flower at the same time as the much more abundant and massive flowering *B. crassifolia* (Frankie *et al.*, 1983). The flowers of *B. crassifolia* are asynchronous, opening from 0530 to 1300 h CST, but this plant is self-compatible (Bawa, 1974), thus the movement of bees within these trees is important to their pollination. Again, only female *Centris* are involved in pollination of this tree. Although males of *C. flavifrons*, *C. inermis* and *C. nitida* commonly use these trees for their territories (Frankie *et al.*, 1989), territories in *B. crassifolia* are defended before, after, as well as during flowering. Although males may chase females from *B. crassifolia*, the importance of this behaviour to the plant's reproductive biology is unknown.

OTHER RESOURCES

In addition to nectar, oil and pollen, the trees provide territorial sites for males and dead wood in which some species of *Centris* nest. The role of trees in providing territorial sites has been described above because of the role the bee territories have in the reproductive outcrossing of the tree, as well as the role in the reproductive biology of the bees.

Three subgenera, *Heterocentris*, *Hemisiella* and *Xanthemisia* nest in holes in dead wood. However, *Centris* are unable to bore their own holes and thus depend on holes provided by other species. What wood boring species are important and if certain tree species are important is presently not known. We do know that each *Centris* species requires a specific range of hole sizes in which to nest (Frankie *et al.*, 1988a). These results would suggest that each wood hole nesting *Centris* species may be dependent on a certain group of wood boring beetles or xylocopids to provide the proper holes. The need for existing holes also suggests that *Centris* must nest in dead wood that is several years old to provide for its use by the wood boring species. Thus, holes of the proper size and location may be in short supply.

Threats to the components of the system

Deforestation and habitat changes

Prior to 1970, the area around what is now Lomas Barbudal consisted of over 20 000 hectares of dry forest (Fig. 3.6), and by 1980 some 10 000 hectares had been cut for agricultural development. By 1990, another 5000 hectares were cut, and today little forest remains outside the 2400 hectare Lomas Barbudal, which was established in 1986, and the Rafael Lucas Rodriguez C. Wildlife Refuge and Palo Verde National Park. While habitat destruction has played a major part in the declining fauna and flora, even the preserved areas are under serious threat. Their continuing threat is due to two factors. One is fire, and the second is the invasion of an introduced grass. These two factors are interrelated through the activities of people in the area.

Fire and introduced grasses

Recently, there have been increasing questions raised about the role of fire in the natural ecology of the Costa Rican dry forest (Janzen, 1986), particularly the savannah. Interviews with old ranchers and farmers in the area indicate that fires occurred only infrequently before large-scale agricultural development took place in the 1960s and 1970s (G.F. Frankie, pers. comm.). When they occurred prior to 1960, the burn intensities were low, and the fires were usually localized. Further, analysis of the vegetation shows little or no adaptation for fire, especially in the area of fruit and seed dispersal (G. Frankie, pers. survey). Some trees do appear to be fire resistant in having a thick bark; whereas others are variably fire susceptible. As described by Boucher *et al.* (1983), the post-conquest savannahs of Costa Rica were dominated by native grasses. These grasses were generally short and during some dry seasons rapidly burned and bee resource trees such as *Tabebuia rosea*, *T. ochracea*, *Dalbergia retusa* and *Cochlospermum vitifolium* could withstand such rapid and low intensity fire. However, the spread of the African pasture grasses such as *Hyparrhenia rufa* (Daubenmire, 1972; Pohl, 1983), known as jaragua, into the tropics (Parsons, 1972, 1976) aided by the beef cattle

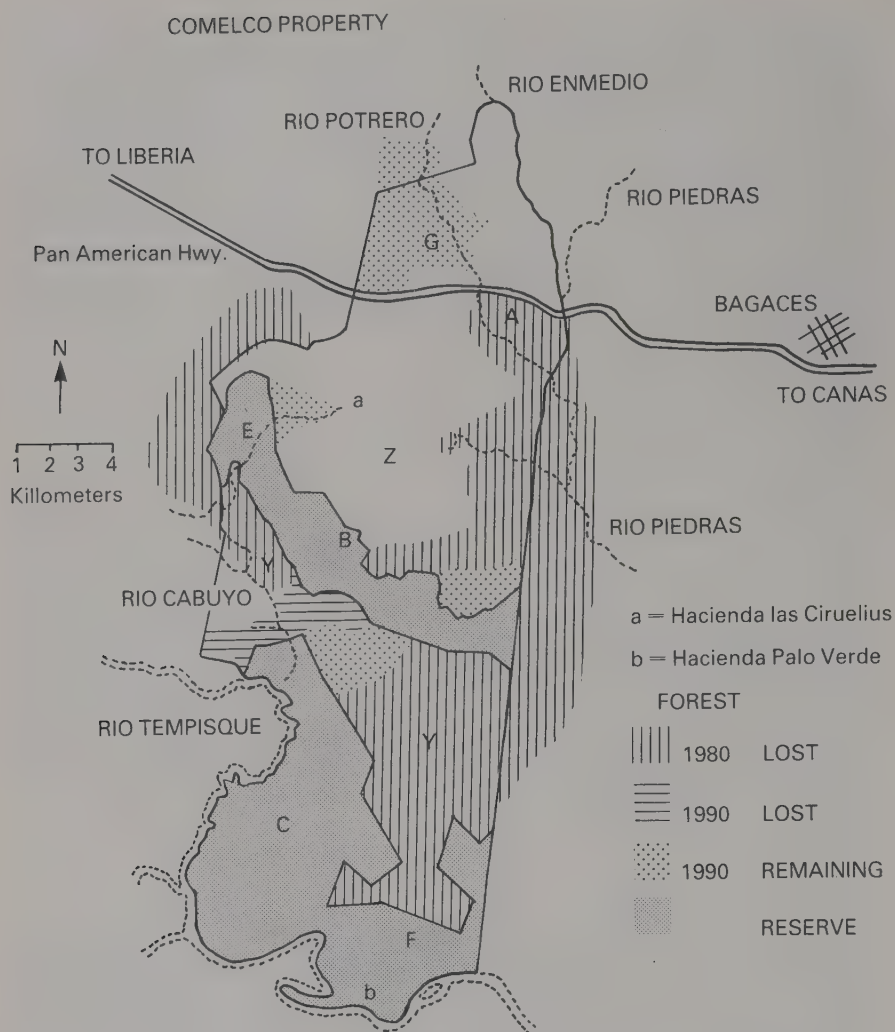


Fig. 3.6. The original Comelco property in Guanacaste Province, Costa Rica shows the changes in forest cover that have occurred since 1970 when all but the area designated Z was forest. By 1980 large tracts of forest were removed. Areas north, east and west of Lomas Barbudal (reserve area enclosing E and B), including Z, are presently pasture with patches of highly disturbed forest. Areas Y cleared south of Lomas Barbudal presently consists of rice fields. Area enclosing C and F is the Palo Verde National Park and Rafael Rodriguez L. Caballero Refuge. Area G is a grassland/oak woodland. Four small undeveloped patches of unprotected forest exist.



Fig. 3.7. The encroachment of jaragua grass (arrow) in the savannah. Note the height of the jaragua grass compared to the native grasses.

industry (Parsons, 1976, 1983) has had a serious and sustained impact even on the protected dry forest. Although jaragua is considered fire resistant (Pohl, 1983), during the dry season in the dry forest life-zone, this grass does burn and when it does, it burns hot. Further, the characteristic westerly trade winds that continually blow during the dry season along with the 2 m height (Fig. 3.7) of the grass (Pohl, 1983) results in intense heat on the downwind side of trees resulting in fire burning through the bark (Janzen, 1986; see also Fig. 3.8A). As a result, the savannah shifts in its composition of trees. Trees such as *T. rosea*, *T. ochracea*, *D. retusa* and *C. vitifolium*, which are important nectar and pollen resources for *Centris*, are particularly susceptible and readily burn. A small number of fire resistant species such as *Byrsonima crassifolia*, *Curatella americana*, *Crescentia alata* (Bignoniaceae), *Godmania aesculifolia* and *Acrocomia vinifera* (Arecaceae) (Parsons, 1975) remain resulting in a shift in favour of the jaragua grass and a few trees, of which only *B. crassifolia* is of particular importance to *Centris*, although *C. americana* is a good pioneer species and can be an important pollen source.

These savannah fires burn to the forest edge where their intensity damages the trees (Janzen, 1986), reducing their shade and providing enough light to allow the jaragua grass to invade a little further into the forest each year. The intense fires slow down at the forest edge due to a change in fuel type. However, the fire continues at a creeping pace into the forest consuming leaf litter and dead trees, and killing one- or two-year-old trees as it goes. When dead trees are reached, the fires grow locally in intensity, often damaging nearby trees. The



direct result of the fire is a reduction in dead wood, and this translates to a loss in nesting sites for *Centris*. Dead wood attracts wood boring insects which in turn make holes that *Centris* and other Hymenoptera eventually use for nesting. Further, the forest opens up as a result of the intense burn spots and this leads to grass invasion and increased temperatures, which *Centris* cannot tolerate during their development. Such problems would not be as serious if they only happened infrequently, but presently fires are occurring almost yearly.

Local people commonly burn to clear their fields, and these fires know no boundaries, often burning into the protected areas. Additionally, carelessness such as the tossing of a cigarette from a car can lead to grass fires. Although efforts to produce fire breaks and other techniques to reduce these fires have been initiated (Sheenan-Stone, 1990), they have only been partially effective. Poachers sometimes set fires within the protected areas, and these fires have occurred more frequently in and around Lomas Barbudal since 1977 when agricultural development began in the area.

Impact of the threats on the components of the system

It is difficult to document the changes that have occurred during the last 15 years when experiments to address such changes were not designed. However, we can use data collected 15 years ago and compare it to similar data collected within the last two years. Secondly, we can compare the vegetation in old photographs to the same area today.

Loss of male reproductive resources

Bees such as *C. flavifrons* prefer to maintain territories in *B. crassifolia* (Frankie *et al.*, 1989) although some other species are occasionally utilized. A 200 hectare site on a private ranch near Lomas Barbudal (area G in Frankie *et al.*, 1983; see also Fig. 3.6), consisted of a pasture with 14 small hills that had been cut, but still supported a few small *B. crassifolia* trees and a number of smaller trees ranging in age from one or two to approximately 10 years. On 4 March 1982, we recorded 16 male territories of *C. flavifrons* in this area, and three female nests were also located. An examination of the surrounding forested areas did not reveal any territories although territories were also located in Lomas Barbudal (area B, Fig. 3.6), a high point in the reserve. The results suggest that *C. flavifrons* defend territories only in select areas characterized by hills. Such 'hill-topping' reproductive displays are reported for many Hymenoptera (Alcock, 1987). On 2 February 1984, we recorded 19 territories in the area G hills. In

Fig. 3.8. (A) The typical burned tree trunk showing damage on the downwind side of tree caused by a dry season fire. (B) A felled tree after a second fire burned through the scar similar to Fig. 3.8(A) caused by an earlier fire.

1986, the trees and even shrubs were cleared and the area G was subsequently completely covered in jaragua and no territorial males have been found in the area since. If certain sites are important to the reproductive success of a species, then destruction of these sites could have a profound impact on the population.

The species *C. adanae* which prefers to defend territories in grass, also prefers elevated land masses for their territorial display (Frankie *et al.*, 1980). Frankie *et al.* (1980) reported that the same areas were used year after year, but they observed a decline in the number of male territories. Further, these declines always occurred in areas that were burned. Such areas were more exposed to wind which may have reduced territorial activity (Frankie *et al.*, 1980), but there was no evidence of an increase of territories in nearby unburned areas.

Loss of female nesting resources

Many *Centris* have specific requirements for nesting sites. For example *C. adanae*, *C. aethytera* and *C. flavifrons* nest in sandy loam soil, generally in open savannah, and their nests are relatively shallow (Vinson and Frankie, 1977, 1988). Such nests are easily disturbed and destroyed by ploughing (Frankie *et al.*, 1988b) and as much of the land has deep sandy loam soil it is likely to be deforested and ploughed (Fig. 3.6Y). Several other species such as *C. flavofasciata* and *C. aethiocesta* nest in nearly pure sand such as beach strand (Vinson *et al.*, 1987; Vinson and Frankie, 1988). Populations of these two beach nesting species are subject to destruction by increasing beach front development.

Fire also has a serious impact on bee nesting. For example, the nests of *C. aethytera* usually contain an average of four to six cells (Vinson and Frankie, 1977, 1991), but in burned areas there was a significant reduction in the number of provisional cells (mean = 0.4 cells/nest), which appeared to be due to two factors. One was a possible increase in predation and parasitism. Nests in burned, open ground were more visible and accessible, and during observations of nest provisioning, predation by birds was recorded on several occasions (Vinson and Frankie, 1991). The second factor involves resources (discussed below).

Fire also has an obvious impact on the availability of holes within wood for nesting. On several occasions trap nest blocks placed in the forested areas to gather data on nest site preference of *Centris* (Frankie *et al.*, 1988a) were destroyed by fire. Similarly, a study of a nesting population of an undescribed species of *Xylocopa* revealed 12 nests in dead twigs of *Godmania aesculifolia* that had died in a previous year's fire. Based on the presence of meconia in completed cells from which adults appeared to have emerged, these 12 nests produced 97 adults. A year later, nine nests had been located a month earlier prior to their emergence and marked, but a fire destroyed all the dead trees and nests with pupae before any analysis could be made. Tree hole nesting *Centris* may be even more susceptible to fire since they require dead wood with pre-existing holes caused by other insects. Secondly, like the xylocopids, the *Centris*

are in the middle or near the end of their nest construction period when these fires occur. The result is the destruction of a large number of provisioned nests of the next generation, and the later the fire occurs the greater the damage to the next generation. In addition there is a reduced potential for adult bees to locate resources needed to nest again before their current generation ends.

Habitat modification on nesting success

Fire has another effect on the bees by altering the microclimate of the forest. As the fire burns through the forest, it burns hot in some patches killing the understorey vegetation and opening up the forest to increased solar radiation. As reported by Frankie *et al.* (1988a; Frankie *et al.*, 1993) the tree hole nesting *Centris* prefer to nest in tree holes in shaded and cooler areas of the forest. In areas exposed to the sun the temperature may reach 32 to 38°C for 5 h, but in shaded areas temperatures are generally 2 to 4°C lower. In the field laboratory where temperatures occasionally reached 38 to 40°C, we experienced 90–95% mortality in our wooden nest blocks particularly of young developing bee larvae (Frankie *et al.*, 1988a).

Loss of bee developmental resources

The destruction of developmental resources is another factor impacting the bee population. For example, in 1989 approximately 3000 hectares of low land forest between Lomas Barbudal and the Palo Verde National Park was cut for agricultural land. Based on a photograph of approximately 16 hectares, 53 *T. ochracea* and 42 *T. rosea* were counted; these trees no longer exist. In two photographs taken in 1976 covering about 2 hectares on the savannah of Lomas Barbudal, four *T. rosea* can be seen in flower. In 1990 these four trees were gone due to fire and no replacement flowering trees could be found in the same area. Trees such as *T. rosea*, *T. ochracea*, *D. retusa* and *C. vitifolium* are particularly susceptible to the jaragua grass fires. As the fire burns through the slow and intense burning jaragua grass fanned by the wind, the wind causes turbulence on the downwind side of the tree trunk that sucks the fire and heat next to the tree resulting in burning through the bark. As described earlier, the fire burns through to the heart wood on one side of the tree (Fig. 3.8A), which leaves a scar of dead wood weakening the tree. However, the next year the fire again fanned by the same wind, in the same direction, results in the dead heart wood of the tree catching fire, generally resulting in felling of the tree (Fig. 3.8B). This tree then becomes fuel for the third year fire, often burning intensely, killing any other trees near by. The result is a continual opening of the forest and invasions of the grass.

An equally serious effect may be the impact of fire on surviving resources. Many important resource trees are lost, but *B. crassifolia* appears more resistant to the fire and remains. However, the fire appears to have a serious impact on oil production by *B. crassifolia*. A significant reduction in oil production was found

in flowers from fire singed trees (Vinson and Frankie, 1991), and the loss of the fire susceptible vines eliminates other oil resources. Further, small regrowth of *C. vitifolium* and the shrub *C. biflora*, which are important pollen sources, are also destroyed during such fires. The loss of either of these resources reduces local nesting.

Loss of pollinators

Flowering trees are generally only pollinated by a select group of pollinators which have evolved with the plant in ways that ensure the movement of pollen from the male part of the flower to a compatible and receptive female flower part. This results in the plant's reproductive success becoming dependent on a select few species of pollinator. The malpighiaceae vines and *B. crassifolia* are dependent on the oil-collecting *Centris* for pollination. The pollen producers such as *C. vitifolium* attract a number of pollen collectors but only the larger solitary bees such as *Centris* and *Xylocopa*, which must collect a lot of pollen and can fly many metres to do so, are effective pollinators. Similarly, many insects are attracted to nectar resources but it is primarily *Centris*, *Xylocopa* and *Gaesischia* which are effective pollinators of these dry season flowering trees.

Thus, three groups of different reward producing trees and some vines are dependent on a restricted group of bees, primarily *Centris*. Further, it is important that these bees occur in numbers to ensure that resources are fully utilized forcing the pollinators to move to other trees, and to ensure mass foraging by bees which increase outcrossing, and to increase the occurrence of territories and nesting activities. However, the bee numbers and variety appear to be decreasing. For example, in 1972 bees were collected between 1100 and 1130h CST from *A. inermis* using a long-handled aerial net (40cm hoop diameter) and sweeping across the tree 6–10 times within 30 seconds. These sweeps, which were repeated six times within 30 min, resulted in the collection of over 70 different species over a period of 3 h of collecting spread over two days. The average number of bees per collecting sweep (30s) was about 70 (Frankie *et al.*, 1976). The percent composition of the total 1972 collection is presented in Table 3.5 which consisted primarily of male *C. adanae* and female *G. exul* along with substantial numbers of *C. aethyctera*, *C. inermis* and *C. nitida*. Using the percent composition of the 1972 total collection we calculated the average number of the more common bee species that were collected during each sweep in 1972 so the results could be compared to similar collections conducted in a similar way at the same time of year and at the same location in 1989. The 1989 collection revealed an average of 37 individual bees per collecting sweep with only *C. adanae* and *C. aethyctera* present in any appreciable and similar numbers. There was a reduction in diversity and the second most common species recorded in 1975, *G. exul*, was absent in 1989. With reduced numbers, such factors as group foraging and rapid depletion of massively produced resources may no longer function in flowering trees, resulting in reduced outcrossing.

Table 3.5. Average number of the more common solitary bees collected during one sweep-net collection from a flowering *Andria enermis* during the same time of the day and year in the same location in 1975 and 1989.

Species	1975 ¹		1989 ²	
	Number	%	Number	%
<i>C. adanae</i>	30	42.8	27	72.9
<i>C. aethyctera</i>	7	9.6	9	24.3
<i>C. inermis</i>	6	7.7	—	—
<i>C. trigonoides</i>	5	6.5	—	—
<i>C. nitida</i>	2	3.3	1	2.7
<i>G. exul</i>	11	15.8	—	—
Other species	10	14.3	—	—
Total	70		37	

¹Average of six samples (data developed from Frankie *et al.*, 1976).

²Average of two samples.

Summary

Although the Lomas Barbudal Biological Reserve in Costa Rica was set aside to ensure the survival of the bees, as well as the other fauna and flora, the survival of this reserve and the remaining Central American dry forest and its diversity will require immediate and decisive management action. The extensive grassland, pastures and savannah, primarily consisting of the introduced jaragua grass along with the frequent fires that help maintain the grass, is slowly encroaching on the remaining forest. The grass shades out the native grasses and many newly germinating tree seedlings. The trees that do manage to survive a year or two are removed by the fires. These fires burn and kill the lower limbs of trees on the forest edge along with the small secondary foliage opening the edge to sunlight providing the jaragua grass the opportunity to invade deeper into the forest. This results in the fire penetrating deeper the next year and so on. The grass even invades openings deeper in the forest beginning the development of grassland within the forest.

These frequent fires also reduce the resources needed by the bees. These include loss of nectar (needed by males to maintain reproductive territories and by females for nesting energy), the loss of male territorial sites, loss of pollen and oil resources needed for nest provision, loss of tree hole nesting sites, increasing the bees exposure to predators and parasites, and increasing their exposure to unfavourable environmental conditions. As these large tree pollinators decline, so too does the pollination of the various large bee-adapted tree and vine-liana species.

What can be done? Several recommendations can be made. One is to allow cattle to feed on the jaragua grass during the wet season, thus reducing the grass while having a minimal impact on small trees. Removal of cattle as the grass becomes less competitive with the trees as the dry season approaches can help the young trees. Protection of the forest, however, generally requires more aggressive means.

Another is the construction and maintenance of fire breaks, particularly between large grasslands upwind of the forest. Reforestation with fast growing tree species in selective locations that produce sufficient shade to prevent grass invasion can result in more permanent fire breaks, if protected during their establishment. However, to maintain the health of the forest and the dry forest ecosystem will require reforestation of much of the surrounding land with a diversity of native trees. Such reforestation projects may need to consider their protection from reinvasion of grass by patches of non-native species that reduce the windswept grass fires from penetrating the regenerated native forest. We believe that careful co-operation between farmers and ranchers, foresters, national park service personnel and conservationists, and biologists, is needed. Such co-operation can result in both the protection of the dry forest ecosystems and interests of the local community.

Finally, effective land management and local action plans need to be developed by the government to protect wildlands. Further, the government land stewards of wild areas must be better trained to accept the task of implementing the management and action plans. They must also build in performance evaluations for these plans. Effective land stewardship in the dry forest is in its infancy as major goals and problems are being identified. Further, the private sector is just starting to take an active, but limited role in land stewardship together with the government. Intelligently combining both forces together should greatly improve the conservation and protection of wildlands.

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Effects of Increasing Land Utilization on Species Representation and Diversity of Aculeate Wasps and Bees in the Semi-arid Areas of Southern Africa

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Introduction

Considering that most species in the world are insects, it is remarkable that in the recent symposium *Biotic Diversity in Southern Africa* (Huntley, 1989) insects are barely mentioned and that the chapter 'Conservation status of the fynbos and karoo biomes' (Hilton-Taylor and Roux, 1989) mentions only three insects, all pest species: the karoo caterpillar *Loxostege frustalis*, the brown locust *Locustana pardalina* and the harvester termite *Hodotermes mossambicus*. Is this perhaps a reflection of a prevalent apathy towards insects and a consequent lack of awareness of their presence unless they are responsible for large-scale destruction? That there is the dawning of a general realization that most species in the world are insects is suggested by Collins (1991) who states that:

In the past five years or so the biodiversity penny has dropped, and it is not just entomologists who now know that insects rule the world, even politicians appreciate the importance of insect diversity and ecology. They are asking what can be done to maintain global diversity? How can it be measured? What are the threats? Where should action be taken?

In order to attempt to address such questions an intimate knowledge of the structuring of ecological systems is required. World-wide the distribution of areas

for which such knowledge is available is very limited. What is presented here concerning the aculeate wasps and the bees of the Karoo, the collective term for the semi-arid areas of southern Africa, is perforce based almost solely upon our investigations undertaken over the past thirty years. Our view and perception of the area is therefore clearly determined by the temporal vantage point at which we find ourselves, a time at which the greater part of the area under consideration has already undergone change as a result of man's activities.

Various levels of diversity have been recognized. Seven levels and types of species diversity were recognized and defined by Whittaker (1977). Three are adapted here to elucidate the interpretation of aculeate wasp and bee diversity. We use one inventory diversity, alpha diversity, which is the number of species in what we term major communities. We also employ two differentiation diversities: beta diversity which is between-habitat diversity within major communities, and delta diversity which is diversity between major communities in different geographic areas.

Thus three basic levels of rarity are recognized: alpha rarity is rarity within a major community; beta rarity is a habitat specialist; and delta rarity is geographically restricted and narrowly endemic.

It is not surprising that the study of diversity in these terms is most advanced for plants. Plants are static, making plot and line sampling relatively straightforward. For small highly mobile animals such as aculeate wasps and bees the task is more complex. Most are nest builders or nest users and so the nest site does give a fixed point of reference within the habitat. The habitat of any one species, however, must satisfy not only its nest site requirements, but also its nesting material requirements and its foraging requirements. A suitable nest site being essential to the existence of a species in an area, nest site characters can be used to establish major community structure patterns. For major community structure and species representation of areas to be comparable all the basic nest site types, that is horizontally presented ground (both friable and non-friable), vertical blanks, suitable plants and stones must be included in each of the areas.

For a comparative study four areas were chosen in the Karoo. A strikingly similar major community structure pattern was established for all areas. Thus, though the sample areas are composed of a variety of interlinked habitats, they can be considered to be comparable units. Comparison of species representation between the four areas in the Karoo will therefore give an indication of delta diversity, and therefore of geographical restriction and of areas of endemism. Furthermore, a comparison within an area between the degree of turnover of species between major nesting situations and an examination of foraging based on plants as the primary energy source does give an indication of beta diversity and therefore of habitat specialization.

Using this preliminary understanding of beta and delta diversity of aculeate wasps and bees combined with an account of land use, an indication of the effects of land use on aculeate wasp and bee diversity in the Karoo is given.

Characterization of the Karoo

The semi-arid areas of southern Africa are here collectively termed the Karoo. This is the area of the Karoo Biome and as defined for the Karoo Biome Project (Cowling, 1986) is constituted of the Succulent Karoo Biome and the Nama Karoo Biome of Rutherford and Westfall (1986) (Fig. 4.1). The Karoo lies in the main to the south of 22°S, and occupies an area of 652 339 km². Within the boundaries of South Africa (including the self-governing states) it occupies 35.1% of the land area, that is 428 015 km² (Rutherford and Westfall, 1986).

The Karoo can be divided into three climatic regions characterized by: (i) predominantly winter rainfall; (ii) predominantly spring and autumn rainfall; and (iii) predominantly late summer rainfall. Plant growth and flowering, and insect activity (Fig. 4.2) are seasonal and linked to the rainfall pattern.

The mean annual rainfall varies from less than 100 mm to 500 mm but is rarely more than 250 mm. Cyclical droughts are a feature of the spring and autumn, and the summer rainfall areas resulting in rainfall decreasing over six- to ten-year periods and increasing over alternating six- to ten-year periods; the length of the periods varying spacially and temporally (synthesized from Novellie, 1988). There are large temperature fluctuations, both daily and seasonal.

The western Karoo lies in the winter rainfall region and is characterized by a noticeable succulent element (and is consequently known as the Succulent Karoo). Seven of Acocks's (1953 and 1975) Veld Types are represented. The central and eastern Karoo lie in the late summer rainfall region and have a markedly lower succulent element (and are together known as the Nama Karoo). Twenty-one of Acocks's Veld Types are represented. The southern, south-eastern and Little Karoo lie in the spring and autumn rainfall region. There is a progressive decrease in the succulent element from west to east. The vegetation of the Karoo as a whole is characterized by dwarf open shrubland dominated by Asteraceae and Mesembryanthemaceae.

Hilton-Taylor and Le Roux (1989) defined the nature of the vegetation of the Succulent Karoo and the Nama Karoo.

The vegetation of the Succulent Karoo is low to dwarf (usually one metre tall), open to sparse (15 to 50% canopy cover) succulent shrubland. This shrubland is dominated by stem and leaf succulents (particularly of the families Mesembryanthemaceae, Crassulaceae, Asclepiadaceae, and Euphorbiaceae), fine-leaved evergreen shrubs and some obligatory deciduous shrubs. Grasses are infrequent and mainly annuals. The mass flowering displays of annuals (mainly Asteraceae) and geophytes (Liliaceae *sensu lato* and Iridaceae) in spring, particularly in disturbed areas, are characteristic. Low trees are common on rocky outcrops and along river courses. The high succulent species diversity is unparalleled elsewhere in the world. This, together with the geophytic and annual taxa, makes the Succulent Karoo a unique biome of international importance.

The vegetation of the Nama Karoo is low to dwarf, open to sparse (see

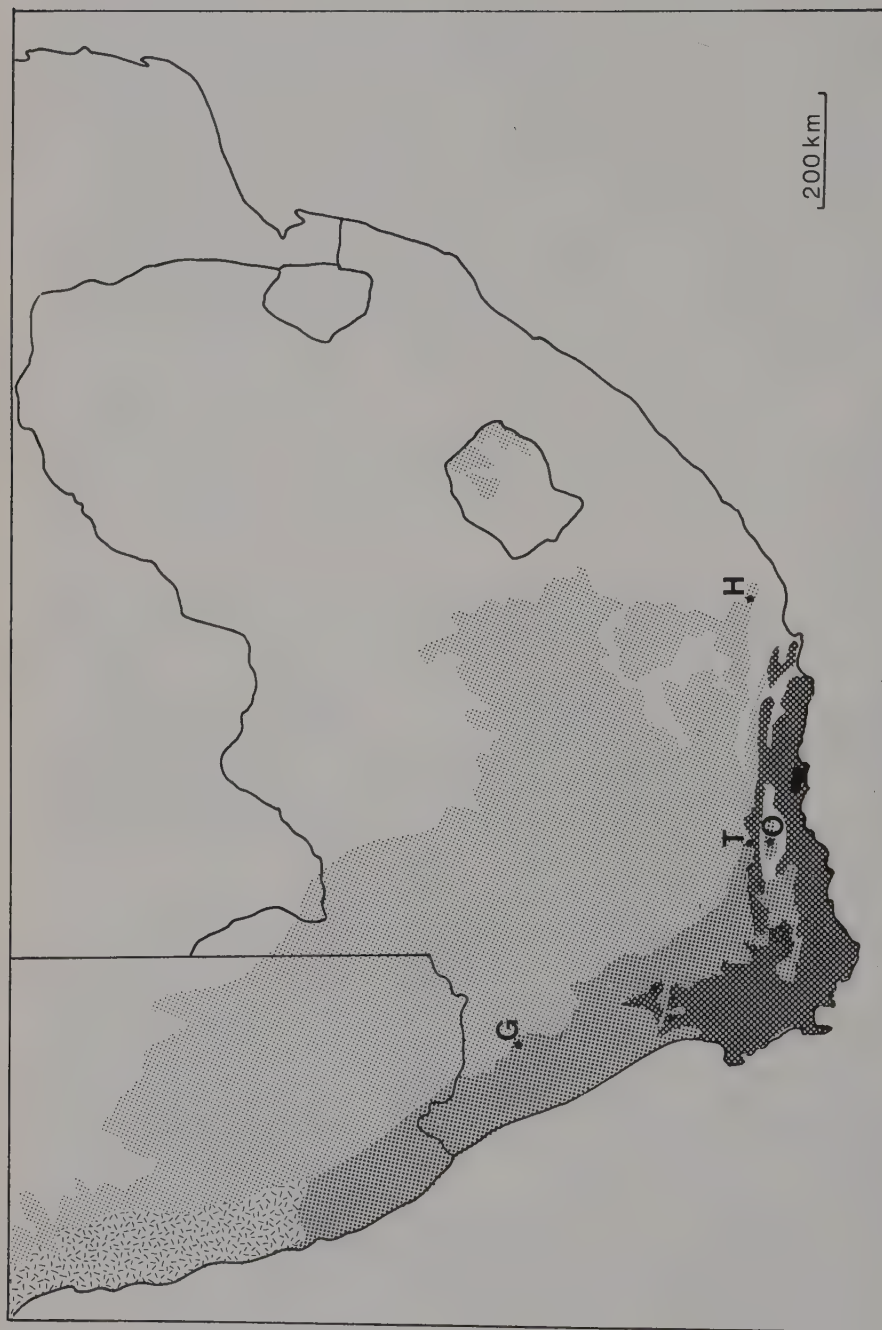


Fig. 4.1. Map of southern Africa showing the extent of the Fynbos (dark grey), Succulent Karoo (medium grey), Nama Karoo (light grey) and desert (speckled) biomes (after Rutherford and Westfall, 1986) and showing locations of the four main study areas. G = Goegab Nature Reserve; T = Tierberg Farm; O = Onverwacht Farm; H = Hilton Farm.

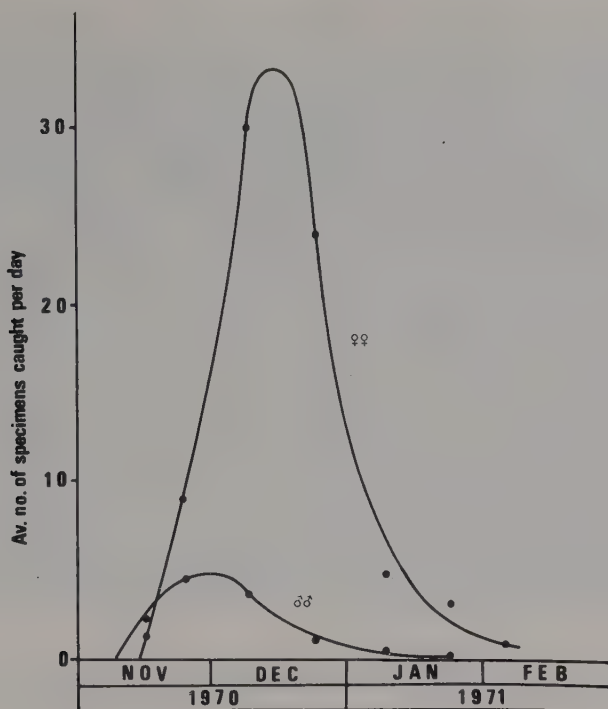


Fig. 4.2. A typical flight period graph for an aculeate wasp in an eastern Nama Karoo area characterized by a predominantly spring and autumn rainfall regime (example *Bembecinus cinguliger* (Sphecoidea: Nyssonidae) from Gess and Gess, 1975). In the western Cape the typical flight period shows a similar pattern but with emergences coming some weeks earlier.

previous definitions), grassy shrubland. This shrubland is dominated by facultatively deciduous shrubs, some leaf succulents and perennial grasses. Grasses become more dominant from west to east. Scattered trees grow on rocky outcrops, low hills and along river courses. The Nama Karoo does not appear to have a species-rich or unique flora. Many of the plant species are shared with the Savannah, Grassland, Succulent Karoo and Fynbos biomes.

The Principal Study Sites

Four sites for intensive study were chosen: the Goegab (formerly Hester Malan) Nature Reserve in Namaqualand; Tierberg Farm in the southern Great Karoo; Onverwacht Farm in the Little Karoo; and Hilton Farm at the easternmost extension of the Karoo (Fig. 4.1). All sampling areas were chosen to include the full

range of nesting situations, horizontally presented ground (areas of both friable and non-friable soil), vertical banks, plants, and stones.

The Goegab Nature Reserve (Fig. 4.3) lies 12km east of Springbok in the Carolusberg, in the region of Namaqualand termed Namaqualand Klipkoppe which is characterized by rocky hills and Eindoon granite domes. The vegetation is classified as Acocks's Veld Type 33, Namaqualand Broken Veld (Acocks, 1953, 1975; Van Rooyen *et al.*, 1979).

Tierberg Farm (Fig. 4.4) to the east of Prince Albert lies immediately inland of both the Outeniqua Mountains and the Swartberg Range in the southern Great Karoo, and Onverwacht Farm (Fig. 4.5), in the Oudtshoorn district, lies between the Outeniqua Mountains and the Swartberg in the Little Karoo. Both areas lie in Acocks's Veld Type 26, Karroid Broken Veld (Acocks, 1953, 1975).

Hilton Farm (Fig. 4.6) is situated 18km WNW of Grahamstown in a south-eastern extension of the Karoo in Acocks's Veld Type 37, False Karroid Broken Veld (Acocks, 1953, 1957).

Altitude, rainfall and wettest seasons are given in Table 4.1.

Major Community Structure

In order to establish a major community structure for the aculeate wasps and bees of the Karoo we devised an ecological-behavioural classification (Gess,



Fig. 4.3. Goegab Nature Reserve in Namaqualand.



Fig. 4.4. Tierberg Farm to the east of Prince Albert in the southern Great Karoo.



Fig. 4.5. Onverwacht Farm in the Oudtshoorn district in the Little Karoo.



Fig. 4.6. Hilton Farm situated 18 km WNW of Grahamstown in the south-eastern extension of the Karoo.

1981) based on:

1. nest situation;
2. the nature of the substrate required for nesting;
3. whether the nest is constructed in or on the substrate;
4. the degree of participation by the nester in the construction of the nest, that is whether the nesters:
 - (i) construct their nests entirely by themselves;
 - (ii) use pre-existing cavities which they modify;
 - (iii) use pre-existing cavities which they do *not* modify (this category is mostly composed of nest 'parasites').

A detailed analysis of the structure of the major community at Hilton Farm based on this classification is given by Gess (1981). A diagrammatic representation of the structure of the community based on 241 species is given in Fig. 4.7.

The structures of the major communities of our four principal study areas based on nest situation only (Figs 4.8a,b,c, and d) show the basic major community structure of the four areas to be very similar indicating that this structure is characteristic of the Karoo.

It is probable that the major community structure established for the Karoo is typical for comparable semi-arid areas at similar latitudes in both the northern and southern hemispheres. This is supported by our findings for a comparable study conducted in the northern Chihuahuan Desert of North America.

Table 4.1. Altitude, rainfall and wettest seasons of the four principal study areas.

Site	Goegab (Springbok)	Tierberg Farm (Prince Albert)	Onverwacht Farm (Oudtshoorn)	Hilton Farm (Grahamstown)
Altitude (m)	1100	1000	450	500
Annual rainfall (mm)	100–200	170	240	350
Wettest seasons	Winter Spring	Spring Autumn	Spring Autumn	Spring Autumn

Geographical Affinities of the Aculeate Wasp and Bee Fauna of the Karoo

Intensive sampling of the aculeate wasps and bees of the four principal study sites was undertaken using Malaise traps, hand nets and trap-nests.

Species representation in the four communities was compared by calculating percentages of similarity and of uniqueness. The percentage species similarity of each community compared with the Goegab Community (Fig. 4.9) and the Hilton Community (Fig. 4.10) was calculated using Sorensen's coefficient of overall similarity,

$$S = 2C/A + B \times 100$$

where S = percentage similarity, A = no. species in sample A, B = no. species in sample B and C = no. species common to both samples.

The percentage species uniqueness of each community compared with all the other communities (Fig. 4.11) was calculated using

$$U = X/Y \times 100$$

where U = percentage uniqueness, X = no. of species not represented in any of the other community samples and Y = the total no. of species in the sample.

From a consideration of Figs 4.9, 4.10 and 4.11 we conclude that:

1. There are considerable differences in species composition between sites. That is, there is considerable delta diversity between sites.
2. The wasp and bee fauna of the southern Karoo is polarized into two main faunal groups, one centred in the west and the other in the east, here represented by the Goegab and the Hilton communities respectively.
3. Between the two extremes lies a transition of overlapping subtraction margins of the eastern and the western faunas, within which lie the Tierberg and the Onverwacht communities.

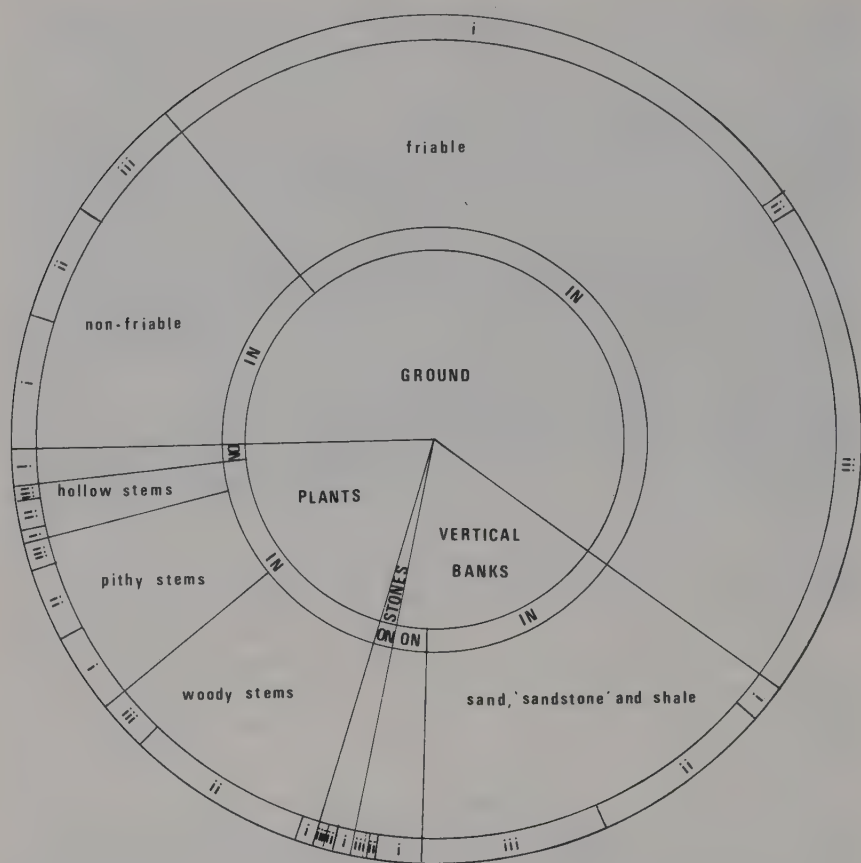


Fig. 4.7. Diagrammatic representation of the structure of a community of 241 species of aculeate wasps and bees at Hilton Farm on the basis of their ethology. The magnitude of the segments is in proportion to the numbers of species involved. The numbers (i, ii, iii) in the outermost ring indicate the degree of participation by the nesters in the construction of the nests, that is whether the nesters: (i) construct their nests entirely by themselves; (ii) use pre-existing cavities which they modify; (iii) use pre-existing cavities which they do *not* modify.

4. The species composition of the community at Tierberg lying at the southern edge of the Great Karoo, inland of both the Outeniqua and the Swartberg mountain ranges shows greater affinity with that at Goegab than with that at Hilton whereas that at Onverwacht in the Little Karoo lying between these mountain ranges shows greater affinity with that at Hilton than with that at Goegab.

5. The species composition of the community at Tierberg shows greater uniqueness than that at Onverwacht.

Species of the western fauna do not have distributions with northern extensions beyond the limits of the Karoo. Of those species not occurring in the eastern fauna as represented by the Hilton site (90% of the species), a very high percentage can be considered to be endemics. Furthermore, from a consideration of the known distributions of these species it can be stated that many of the endemics have very restricted distributions, that is high delta rarity.

By contrast many of the species of the eastern fauna have distributions with north-eastern extensions, some species ranging into Kenya or even Ethiopia. There is therefore a much lower level of endemism in the eastern fauna. However, from a consideration of known distributions of species it is probable that there are some eastern Karoo endemics (S.K. Gess, 1993).

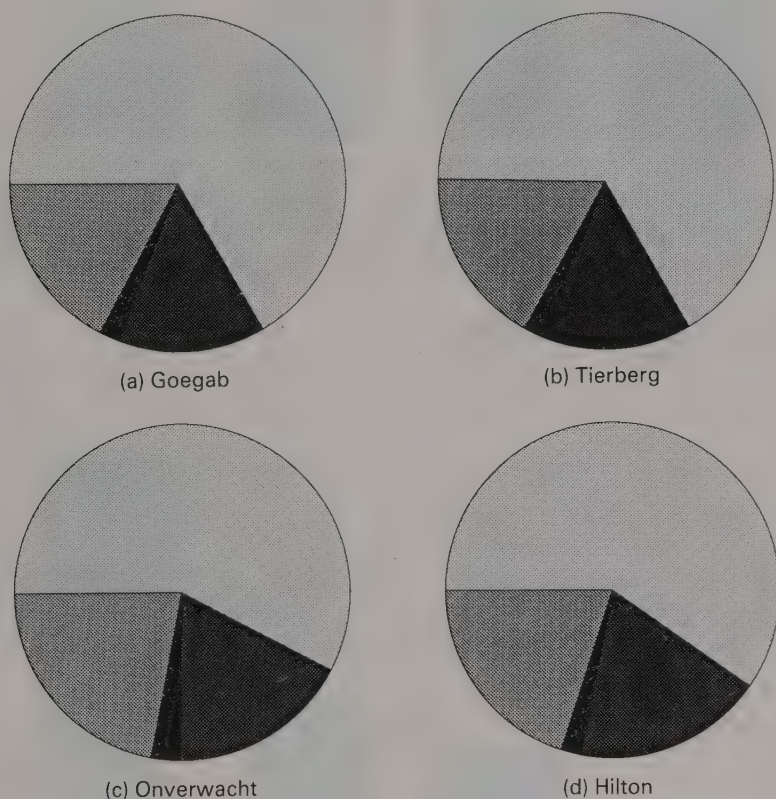


Fig. 4.8. Diagrammatic representations of the structure of the communities of aculeate wasps and bees on the basis of nest situation at: (a) Goegab Nature Reserve, (b) Tierberg Farm, (c) Onverwacht Farm, (d) Hilton Farm. The magnitude of the segments is in proportion to the numbers of species involved. Horizontal ground – light grey; vertical banks – dark grey; stones – black; and plants – medium grey.

Percentage similarity

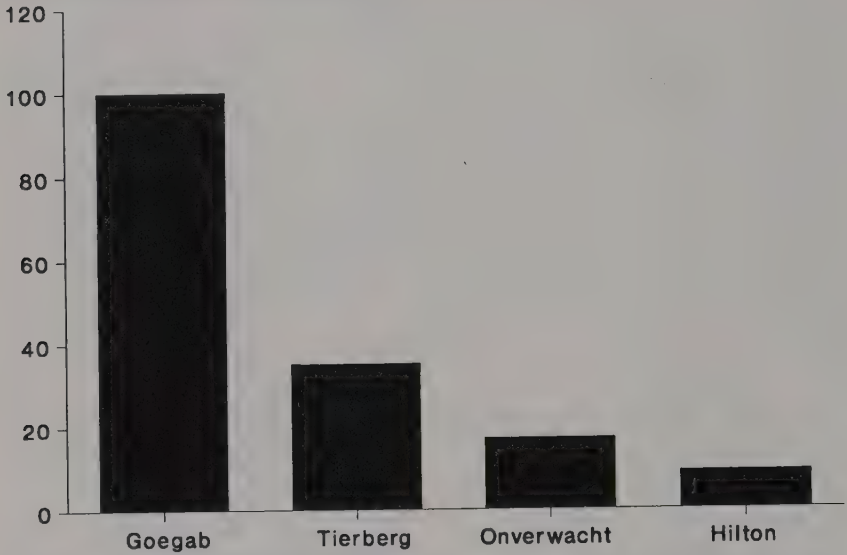


Fig. 4.9. A bar graph comparing the percentage species similarity of the major community of aculeate wasps and bees of Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm compared with that of Goegab Nature Reserve.

Percentage similarity

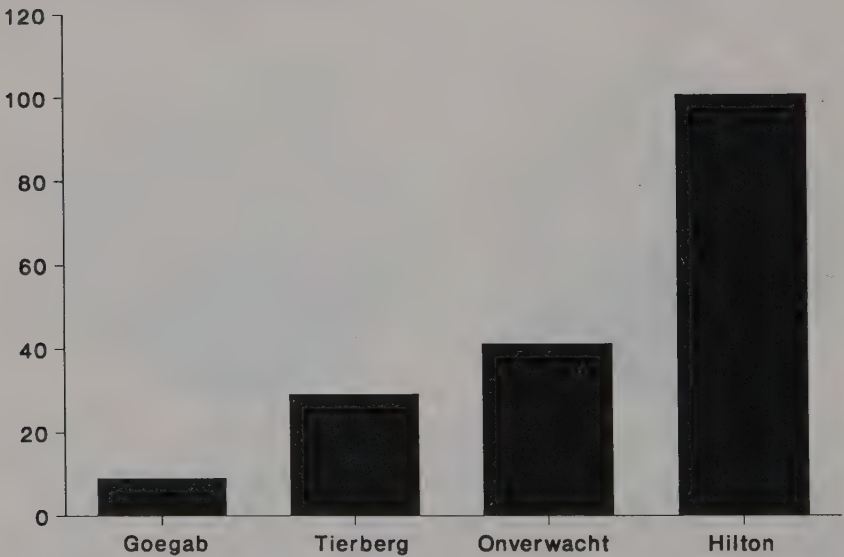


Fig. 4.10. A bar graph comparing the percentage species similarity of the major community of aculeate wasps and bees of Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm compared with that of Hilton Farm.

Percentage uniqueness

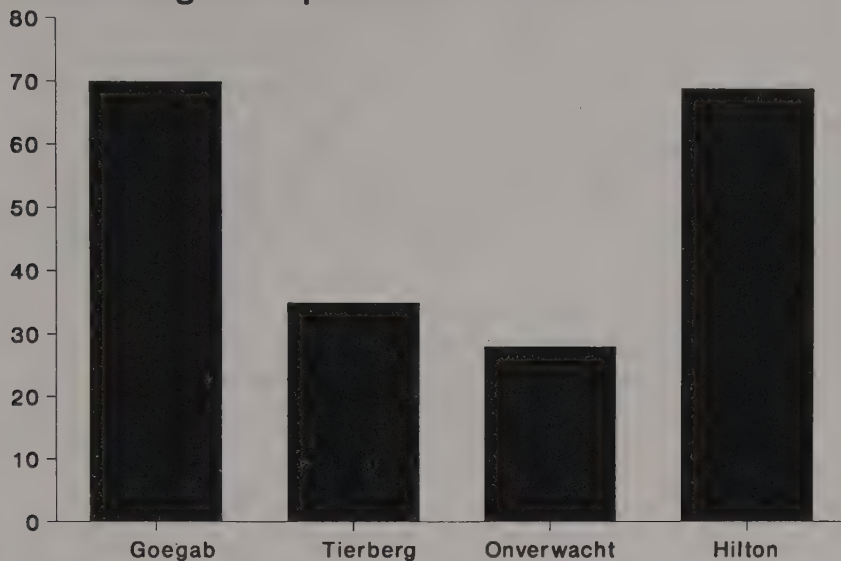


Fig. 4.11. A bar graph comparing percentage species uniqueness of the major community of aculeate wasps and bees of Goegab Nature Reserve, Tierberg Farm, Onverwacht Farm and Hilton Farm.

The subfamily Masarinae (*sensu* Carpenter, 1982) is notable for its high level of endemism. Of the 140 species known from southern Africa all are endemic to this region and all but a few are endemic to the Karoo. Many are restricted to the western fauna and among these there are notable examples of narrow endemism.

The greater uniqueness of the species composition of the community at Tierberg as compared with that at Onverwacht might be explained by the presence of species derived from a northern fauna which probably does not extend south of the Swartberg Range. A preliminary sampling of the aculeate wasp and bee fauna of the southern Kalahari at the interface between the Karoo and Savannah biomes lends support to this hypothesis.

Comparative Overview of Nesting in the Four Basic Nesting Situations

Horizontally presented ground

Soils utilized by ground nesters may be divided into two broad types, friable soils and non-friable soils. Friable soils are easily crumbled and nesters in these soils are able to excavate their nests without the aid of water. Non-friable soils are not easily crumbled and are therefore not easily excavated. They contain a clay

element which makes them malleable when mixed with water. Nesters in these soils generally make use of water transported by themselves to their nest sites for softening the ground and a water source is therefore required. Taking the semi-arid areas as a whole, species nesting in friable soil far outnumber species nesting in non-friable soil.

By far the largest number of species of nest excavators in friable soil belong to sphecoid families. At Hilton 67 species of friable soil nesters were sphecoids, as compared to nine species belonging to other families. Friable soil most favoured for nesting is water deposited sand of the flood plains and dry water-courses.

Species excavating nests in non-friable soil using water are in the main species of Masarinae and Eumeninae. This type of nest excavation is exceptional for Pompilidae and Sphecoidea, only two species each being known to nest in this way, and seems to be similarly uncommon for bees in the area under consideration.

Non-friable soil generally underlies the sand of the watercourses and flood plains so that as the ground rises at some little distance from the watercourses non-friable soil is exposed. Nest excavators in non-friable soil generally nest relatively close to water sources but some species will fly up to about 300 m to fetch water for nest excavation. Some *Ceramius* species (Masarinae) and *Bembecinus cinguliger* (Sphecoidea: Nyssonidae) which nest in aggregations may nest in thousands in a wide band flanking a watercourse (Gess and Gess, 1975, 1988a). Other species of *Ceramius* are never abundant and the two pompilids, *Dichragenia* species, never form aggregations and are never found in large numbers (Gess and Gess, 1974, 1976b). Apart from watercourses as available water sources for nesting wasps and bees, there are in the semi-arid areas springs which form natural pools.

For both horizontal ground soil types pre-existing cavity users and 'parasitic' species are present in addition to the nest excavators. Clearly the availability of nesting sites for these species is directly linked to that of the burrow excavators though not all cavities used are the burrows of wasps or bees. Abandoned burrows of other insects such as a ground nesting cockroach, *Pilema thoracica*, are also utilized (Gess and Gess, 1982). There are in addition in the friable soils 'parasitoids' of the families Scoliidae and Tiphidae which are solely dependent on the presence of their coleopteran hosts.

No species are shared between horizontally presented ground and any other nesting situation.

Vertical banks

Wasps and bees which nest in association with vertical banks may be divided into those which nest within the banks, in cavities either excavated by themselves or in pre-existing cavities, and those which nest on vertical banks and use the latter solely as a raised support to which to attach their aerial nests.

Vertical banks of compacted friable soil, non-friable soil and rock are to be found naturally occurring principally along watercourses and artificially along roadsides, the sides of quarries and some kinds of man-made walls.

The assemblages of aculeate wasps and bees nesting in vertical banks are much smaller in species numbers than those nesting in horizontally presented ground. The numbers of nest excavators are usually far outnumbered by pre-existing cavity users; at Hilton the ratio is 4:20. Pre-existing cavities in banks are mostly the abandoned burrows of wasps and bees, however, in shale banks the cracks between layers of shale are utilized.

There is no overlap between nesters in vertical banks and nesters in horizontal ground nor between nest excavators in vertical banks and nest excavators in plant tissue. There is, however, some overlap between users of pre-existing cavities in vertical banks and users of pre-existing cavities in plant tissue and therefore also between 'parasitic' species nesting in these situations. In addition there is overlap between aerial nesters on vertical banks, plants and stones.

Plants

Wasps and bees which nest in association with plants may be divided into those which nest within plants, in galleries within plant tissue, and those which nest on plants and use the latter solely as a raised support to which to attach their aerial nests.

With respect to those species which nest in plant tissue, it is necessary that the parts of the plants concerned should be thick enough to contain the nesting galleries and that the hollow parts should retain their physical structure. Plant stems may be classified as woody, pithy or hollow. The nature of each stem determines which species may be able to prepare galleries within it and each of the three stem types therefore has associated with it species peculiar to itself. Most excavators of galleries in stems are anthophorid bees and most choose dead dry stems. The choice of live green stems by *Dasyproctus* species (Sphecoidea: Crabronidae) (Gess, 1980) is unusual.

In karroid areas plants with suitable woody stems are generally available only in the riverine bush along watercourses. The most notable pithy stems are inflorescence stems of *Berkheya* species (Asteraceae) and *Aloe* species (Liliaceae). Other pithy inflorescence stems favoured are mainly of species of Iridaceae and Liliaceae. The most notable hollow stems are the culms of the reed *Phragmites australis* (Poaceae) which occurs in thickets fringing the banks of many of the perennial to semi-perennial watercourses.

Nesters in pre-existing cavities in plant tissue exceed cavity excavators in species numbers. Such wasps and bees make use of the abandoned burrows of gallery excavators and also make use of the borings of other insects such as beetle larvae, most notably those of Cerambycidae. There is considerable overlap by these pre-existing cavity users between the three different types of plant tissue. Consequently there is also an overlap in the 'parasitic' species.

There is no overlap between nesters in plant tissue and nesters in horizontally presented ground nor between nest excavators in plant tissue and nest excavators in vertical banks. There is, however, some overlap between users of pre-existing cavities in plant tissue and users of pre-existing cavities in vertical banks and therefore also between 'parasitic' species nesting in these situations. In addition there is overlap between aerial nesters on plants, vertical banks and stones.

Stones

In karroid areas stones are the least used of the four nesting situations. It is clear therefore that this nesting situation is of little importance with respect to the nesting of the communities as a whole. However, it must be taken into consideration that all nests associated with stones are aerial in nature and that a true assessment of the status of this nesting situation can only be arrived at by comparison with the status of aerial nesting associated with other nesting situations. In fact, though smaller, the number of species constructing nests on stones is comparable to the number of species constructing nests on vertical banks and on plants.

As in other situations aerial nests, when vacated by the species which constructed them, become available for nesters in pre-existing cavities and both the nests of the nest constructors and the users of pre-existing cavities support 'parasitic' species.

Plants as a Primary Energy Resource – Direct and Indirect Associations

Direct associations between aculeate wasps and bees and plants as an energy resource fall into two categories – adult nourishment and larval provision. Indirect associations are almost entirely in the category of larval provision.

None of the aculeate wasps and bees feeds directly on the vegetative parts of plants. Flowers are the main source of nourishment for the majority of adult aculeate wasps and bees, as they are nectar feeders. Bees and masarine wasps in addition depend on flowers for larval provision as their young are fed pollen and nectar.

Generally speaking wasps are attracted in large numbers and great diversity to whatever suitable plants may be in flower. Extremely popular are plants with small, white, cream or yellow flowers presented in heads. Among those particularly favoured in the semi-arid areas of southern Africa are *Acacia* spp. (Mimosaceae), *Maytenus* spp. (Celastraceae), *Asclepias* spp. (Asclepiadaceae) and various umbellifer species (Apiaceae) (Gess and Gess, *Catalogue of Flower Visits by Aculeate Wasps and Bees*, unpublished). It is noteworthy that masarine wasps are almost entirely absent from samples of wasps from such plants.

A recent study of flower visiting by masarine wasps (S.K. Gess and F.W. Gess, 1989a), in which records for 69 species belonging to six of the seven genera of southern African masarines were given, showed that the masarine wasps exhibit a high degree of oligolecty. These records show the percentages of species associated with particular plant families to be: Mesembryanthemaceae 51%, Asteraceae 28%, Campanulaceae 12%, Scrophulariaceae 5%, Fabaceae 3% and Liliaceae 2%. A consideration of the guilds of insects visiting the same flowers as the masarines and a comparison of the behaviour of masarines and of the other members of these guilds indicates that the masarines are important potential pollinators, suggesting that not only is the presence of particular plants of importance to the masarines but that they are of importance to the plants which they visit. This view is supported by a study of the association of a North American masarine, *Pseudomasaris vespoides*, with flowers of *Penstemon* species (Torchio, 1974).

Bees show a wide range from polylectic to oligolectic to monolectic species. It is generally recognized that levels of oligolecty are higher in semi-arid areas than in mesic or moist tropical areas (Michener, 1979). Michener suggests that where flowers tend to be synchronized, and where many kinds of bees have overlapping short seasons of flight so that seasonal segregation is impossible, there are advantages in oligolecty, which divides the available food resources among some species and reduces interspecific competition for those resources. Michener, however, also observes that sometimes oligolectic bees appear to play no role in the pollination of their host plants, in effect being parasites, and that in these cases pollination is carried out by polylectic species. Our bee/flower data have yet to be fully analysed, however, from our observations oligolectic bees which seem most probably to have a mutualistic association with the flowers which they visit are species of Melittidae.

Aculeate wasps do not themselves feed on the vegetative parts of plants. The majority of species provision their young with insect or spider prey and therefore depend ultimately on plants as they are the direct energy resource of the phytophagous prey species and the indirect energy resource of the predatory prey species.

A wide range of both phytophagous species and predatory species are taken by aculeate wasps as a group (Tables 4.2 and 4.3). At the specific level, however, there is considerable specialization in the choice of prey. There are no generalists, the range of prey of any one species being restricted at least to order. All degrees of specialization are exhibited from order down to species.

Aculeate wasps like all predators in an ecological system must play a role in maintaining the checks and balances on the populations of the species upon which they prey.

Table 4.2. List of phytophagous insect prey of aculeate wasps, grouped according to their feeding behaviour and with the numbers of species of wasps preying upon them indicated, recorded from Hilton Farm.

Prey role	Prey order	Prey family	Aculeate wasp family and no. of spp.
Sap feeders	Hemiptera	Membracidae	Nyssonidae 2
		Cicadellidae	Nyssonidae 6
		Fulgoridae (<i>s.l.</i>)	Nyssonidae 4
		Aphididae	Pemphredonidae 1
		Cercopidae	Nyssonidae 1
		Pentatomidae	Astatidae 1
Gum feeders	Dictyoptera	Blattidae	Ampulicidae 1
Foliage feeders	Lepidoptera	Psychidae	Eumenidae 2
		Tortricidae	Eumenidae 1
		Pyralididae	Eumenidae 6
			Sphecidae 1
		Geometridae	Eumenidae 3
			Sphecidae 3
		Lasiocampidae	Sphecidae 1
		Noctuidae	Sphecidae 8
		Arctiidae	Sphecidae 1
		Pieridae	Sphecidae 1
		Lycaenidae	Sphecidae 2
		Various unspecified	Eumenidae 5
	Coleoptera	Chrysomelidae	Eumenidae 1
			Philanthidae 1
		Curculionidae	Philanthidae 4
	Orthoptera	Acrididae	Sphecidae 1
			Larridae 1
			Nyssonidae 1
		Lentulidae	Larridae 2
			Nyssonidae 1
		Gryllidae	Larridae 2
		Tettigoniidae	Sphecidae 4
		Acrydiidae	Larridae 1
		Pyrgomorphidae	Larridae 1
			Nyssonidae 1
		Pamphagidae	Nyssonidae 1
Flower/ inflorescence feeders	Coleoptera	Phalacridae	Philanthidae 1
		Scarabaeidae	Philanthidae 2

Prey role	Prey order	Prey family	Aculeate wasp family and no. of spp.
Pollen and nectar feeders	Hymenoptera	Apidae	Larridae 1 Philanthidae 1
		Halictidae	Philanthidae 3
Stem and root feeders	Coleoptera	Buprestidae	Philanthidae 1
		Scarabaeidae	Tiphiidae 16
			Scoliidae 11

Table 4.3. List of spider and non-phytophagous insect prey of aculeate wasps, with the numbers of species of wasps preying upon them indicated, recorded from Hilton Farm.

Prey role	Prey order	Prey family	Aculeate wasp family and no. of spp.
Predators of insects	Dictyoptera	Mantidae	Larridae 2
	Hymenoptera	Tiphiidae	Larridae 1 Philanthidae 2
	Diptera	Asilidae	Nyssonidae 1
	Araneida	Various unspecified	Pompilidae 10 Sphecidae 4 Larridae 5
Blood suckers as adults	Diptera	Tabanidae	Nyssonidae 1
		Simuliidae	Crabronidae 1
Parasites of insects	Diptera	Bombyliidae	Crabronidae 1
			Nyssonidae 1
		Conopidae	Nyssonidae 1
		Tachinidae	Nyssonidae 2
	Hymenoptera	Bethylidae	Philanthidae 1
		Pteromalidae	Philanthidae 1
		Braconidae	Philanthidae 1
		Mutillidae	Philanthidae 1
Scavengers as larvae	Diptera	Calliphoridae	Crabronidae 1
			Nyssonidae 1
		Stratiomyidae	Nyssonidae 2
		Muscidae	Crabronidae 1 Nyssonidae 1

Land Use

Land use in the context of this chapter is restricted in the main to agriculture, that is stock farming and the cultivation of crops, and does not therefore include mining, transport or habitation.

Man as a migratory hunter gatherer in the Karoo is considered to have lived in natural balance with his environment. Although he had settlements which resulted in localized changes in the vegetation which persisted over at least 700 years (Sampson, 1986), he did not restrain the indigenous mammals nor introduce exotic species, nor did he cultivate crop plants. No domestication or herding of indigenous mammals occurred.

Herders of exotic species, sheep, goats and cattle entered the Karoo area from the north. The prehistory of Stone Age herders in the Cape Province is reviewed by Klein (1986). It is believed that domestic stock were introduced to the western and southern Cape at or shortly after 2000 BP. The best documented stock in the western and southern Cape are sheep. Cattle occur much less often and may have been introduced somewhat later than sheep (?1600–1500 BP). Goats may have been relatively abundant in the north-western Cape, at least after 800 BP. At Bethelsklip in the Succulent Karoo they have been identified from between about 800 BP and 360 BP (Webley, pers. comm.). Webley (1986) postulated that the Namaquas aggregated in large groups around permanent waterholes in the dry summer months and split into minimal herding units during the wet winter months. The missionary Shaw (1841) reported that the Namaquas who resided in the area of the Leliefontein mission station moved seasonally between the Kamiesberg (in the Succulent Karoo) in the summer and the coastal Sandveld in the winter.

These early herders do not seem to have penetrated into the Nama Karoo to any appreciable distance to the south of the Orange River or to the north of the southern Cape. Furthermore, there does not seem to have been penetration of the area by the Iron Age agropastoralists coming down the east coast from the north. It would therefore appear that this area had not been subject to grazing by exotic domestic stock before these were introduced into the area by European pastoralists in the early eighteenth century.

By the end of the nineteenth century the vast herds of naturally occurring grazing and browsing mammals had been shot out to give way to large-scale stock farming. With the introduction of boreholes and windmill pumps it became possible to graze stock throughout the region on a year-round basis. This was followed by the fencing of farms in the early twentieth century.

The reduction in the numbers of indigenous large mammalian herbivores, their altered patterns of dispersion and their replacement with domestic stock resulted in substantially altered intensities and patterns of defoliation which must have resulted, in turn, in large-scale changes in the vegetation. Unfortunately these changes are inadequately documented.

The Great Karoo, here taken in its widest sense to include all the karroid areas inland of the western and southern escarpments, now supports a profitable small stock industry which is in the main based on natural pastures. To a limited extent these are supplemented by the cultivation of lucerne pastures and lucerne hay. Lucerne production is restricted almost entirely to the generally very limited irrigable areas along watercourses. Large-scale crop production in the Great Karoo is mainly restricted to the north along the Orange River, where irrigable land is more extensive than elsewhere. There grapes, for drying and to a lesser extent wine production, are being increasingly cultivated, as too is cotton.

The Little Karoo, lying between the southern coastal mountains and the southern escarpment, is largely farmed for deciduous fruit with the Oudtshoorn area being the centre of ostrich farming. The ostriches, in the main, are pastured on lucerne lands in the irrigable river valleys.

The karroid areas to the west of the western escarpment can be divided into two areas, Namaqualand to the north of and including the Van Rhynsdorp district, and the Olifants River Valley to the south. Namaqualand is principally given over to small stock farming with, to the south of Springbok, opportunistic small-scale grain production relying on winter rain. The greater area of the Olifants River Valley lies in karroid vegetation, however, the river rises in fynbos to the south in the Citrusdal district and passes through a mosaic of karroid scrub and dry fynbos in the Clanwilliam district (Moll *et al.*, 1984). The river is strong flowing and perennial making the area ideally suited to irrigation farming. By 1732 European farmers were well established along the Olifants River as far north as its confluence with the Doorn River. With the construction of the Bulshoek Dam in 1922, the Clanwilliam Dam in the 1930s and a system of canals the valley has been intensively developed for the large-scale production of citrus fruit, deciduous fruit, vegetables and vines. In the Vredendal district alone there are today more than 800 active land owners involved in the State's irrigation scheme and the largest co-operative wine cellar in the southern hemisphere.

Discussion of the Likely Impact of Land Use

Factors affecting species representation and diversity of aculeate wasps

The major community structure found to be typical for the Karoo is basically dependent upon the availability of the four main nesting situations described above. For those species excavating nests in non-friable soil as well as for those species using mud in the construction of their nests water is an additional requirement. The species composition of communities is in addition basically dependent upon the species composition of the vegetation, it being the primary energy resource used by aculeate wasps and bees, phytophagous prey species, and indirectly by predatory and parasitoid prey species.

Certain changes in habitat can therefore be expected to produce a noticeable effect on the aculeate wasp and bee fauna. These are as follows.

1. *Changes in availability of nesting sites.* Changes which cause the reduction or loss of nesting sites will result directly in the reduction of population size or loss of species which require those sites to survive in a given area and indirectly in the reduction of population size or loss of species which are nest parasites, parasitoids of the nest originators and species which subsequently use the abandoned cavity.

Changes which create or increase nesting sites will have the converse effect.

2. *Changes to water sources.* Changes which make water or mud unavailable will result directly in the loss of species requiring these resources for nest excavation, nest construction or cavity modification and indirectly the loss of species which are nest parasites, parasitoids of the nest originators and species which subsequently use the abandoned cavity.

Changes which make water or mud available will have the converse effect.

3. *Changes in vegetation.* Loss of, reduction in abundance of or increase in abundance of species will result directly from loss of, reduction in or increase in abundance of, respectively, plant species which are a direct source of provision in the form of pollen and or nectar to monoleptic species, and to oligolectic and polylectic species, if no other suitable plant species are present in the area under consideration.

Similarly, loss, reduction or increase in abundance of species will result indirectly from loss, reduction or increase in abundance, respectively, of the food plants of insects which are the sole prey of particular species of aculeate wasps or are the food plants of the prey of the prey of particular species of wasps.

Loss, reduction or increase in abundance of aculeate wasps or bees as a result of changes which do not affect their 'host' plants or prey will in turn have a variety of effects on these plants and insects, the degree of which will depend upon the nature of their interactions. For example, the nature of the effect of the loss of a flower visitor will depend upon whether the visitor is a destructive visitor or a potential pollinator and, if a potential pollinator, whether the plant is dependent upon its species for pollination. The effect of the loss of a predator will depend upon whether the prey was a phytophagous insect, a predator, blood sucker, scavenger or parasite.

Species most vulnerable to localized loss are clearly those which are the most specialized with respect to their habitat requirements, that is those species with a high degree of beta rarity, and those which are most vulnerable to total extinction are those endemics with very limited distributions, that is those species with a high degree of delta rarity. Clearly loss of habitat diversity will result in a loss of alpha diversity.

Stock farming

The impact of small stock farming on the environment is variable. Variations in rainfall and vegetation dictate different choices of breed of goats or sheep and the number of head which can be supported. Furthermore, which animals are run has a profound effect upon which plants are fed upon. Whether or not rotation is practised and what pattern of rotation is followed further affect the vegetation. For example, in the Nama Karoo long-term experimental grazing treatments have shown that on plots grazed in the summer only there is a marked increase in the dwarf shrub and decrease in the grass element, whereas on plots grazed in the winter there is a marked decrease in the dwarf shrub element and increase in the grass element (Roux and Theron, 1987). Furthermore, drought may cause high mortality of some species which, in the absence of continuous grazing, would re-establish after good rains. However, under current grazing practices, local extinction of species after drought is not uncommon, resulting in possibly irreversible changes in vegetation structure and composition (Roux and Theron, 1987). Many studies have aimed at assessing grazing capacities, especially since the launching of the National Grazing Strategy in 1985. Nearly all studies reflect excessive stocking rates, which together with injudicious veld management, is the cause of widespread degradation. It has been estimated that as much as 60% of the veld is currently in a poor condition (Scotney, 1988). The number, nature and distribution of watering points is also variable and brings about different patterns of soil trampling. Clearly such variations in farming practice have a profound effect on the resources available to aculeate wasps and bees.

Selective grazing or browsing bringing about changes in the vegetation in turn brings about changes in available provision be it insect, spider or pollen and nectar. These changes must inevitably bring about changes in the species composition of the aculeate wasp and bee communities. How extensive these changes are will govern the degree of overall loss of species diversity. The area around Garies in Namaqualand, previously known as a good collecting area for ground nesting species, has in recent years been singularly unproductive. The ground has been severely damaged as a result of trampling by small stock, making nesting by ground nesters impossible. Furthermore, the species composition of the vegetation has been seriously affected, there having been a marked reduction in species diversity, the dominant plant now being *Galenia africana* (Aizoaceae). Owing to the fact that small stock do not utilize it, this plant, which is a pioneer, has increased and is now dominant in much of Namaqualand and the other semi-arid winter rainfall areas (Le Roux and Schelpe, 1988).

Field experience has repeatedly demonstrated to us that *Galenia africana* is a plant that is unproductive of both phytophagous insects and flower visiting insects. It would appear to be as unattractive to insects as it is to small stock. In areas where it has become a dominant plant there will consequently have been a reduction in population sizes of, and almost certainly a reduction in species diversity of, insects including aculeate wasps and bees. It is possible that the

dramatic reduction in the populations of potentially important flower pollinating species, such as masarine wasps and solitary bees, may result in a reduction in seed set by their forage plants resulting in further loss of plant species diversity and consequently of insect diversity.

Typically the Nama Karoo vegetation comprises three major components, the primary matrix, the secondary component and the ephemeral component (Roux and Theron, 1987). The primary matrix is interspersed with the unstable but highly resilient secondary component. Under grazing stress dwarf shrubs of the secondary component, which are unpalatable and are by nature pioneers, increase and spread. Notable among these species is *Chrysocoma ciliata* (= *C. tenuifolia*) (Asteraceae). If one compares the insect guilds associated with this plant with those associated with the superficially similar dwarf shrub *Pentzia incana* (Asteraceae) of the primary matrix, one finds that not only is it unpalatable to stock but that it supports relatively few insects. In a notable series of studies of life histories of lepidopterous species in karroid areas of the eastern Cape Province Taylor and Cresswell (1940) and Taylor (1946, 1949, 1950, 1951, 1953, 1957, 1965) recorded *Pentzia incana* as the food plant of caterpillars of twelve species spread over eight families whereas *C. ciliata* was not listed once.

Studies at Hilton Farm have identified *Pentzia incana* as the host plant of a range of phytophagous species used by aculeate wasps for provisioning their young. Among these are the caterpillars of a species of Psychidae hunted by *Parachilus insignis* (Eumeninae) (Gess and Gess, 1976a) and *P. capensis* (Gess and Gess, 1988b), those of *Loxostege frustalis* (Pyralidae) hunted by *Euodynerus euryaspilus* (Eumeninae) (Gess, 1981; Gess and Gess, 1991), and those of *Bombycopsis indecora* (Lasiocampidae) and *Cucullia nigrilinea* (Noctuidae) hunted by *Ammophila dolichodera* (Sphecidae) (Weaving, pers. comm.). A number of undetermined species of small sap sucking Homoptera (Cicadellidae and Fulgoroidea) found on the plant are hunted by *Bembecinus cinguliger* and *B. oxydorcus* (Nyssonidae) (Gess and Gess, 1975) and possibly also by *B. braunsi* and *B. haemorrhoidalis*. Clearly a change in the balance of *P. incana* and *C. ciliata* will result in a change in wasp prey availability and thus a change in population sizes of wasps utilizing this prey.

The surface structure both of friable and non-friable soil is rapidly destroyed by excessive trampling so that not only existing nests are made unusable but nest initiation becomes impossible. *Bembix bubalus* nesting successfully in thousands in the Oudtshoorn district in a relict, undisturbed area of friable soil in one year was found to be attempting unsuccessfully to excavate nests at the same site in the following year (S.K. Gess and F.W. Gess, 1989b). The area had been so badly trampled that the wasps' efforts at excavation were in vain, the substrate having become too unstable. If a species is widespread and such disturbance is patchy, no overall drop in the population size of the species will occur, however, if the species has a limited distribution and the disturbance is extensive there may be a serious reduction in population size or even a loss of the species.

Watercourses in the stock farming areas are generally lined with taller shrubs or even trees. The woody stems of these plants provide nesting sites for wasps and bees which nest in woody plant tissue. Users of pre-existing cavities far outnumber cavity excavators. They utilize not only the disused burrows of nest excavating bees but also abandoned borings of the larvae of beetles, notably Cerambycidae – all cavities being in dead wood. In karroid areas there is a shortage of fuel and so wood gathering is actively pursued. This removal of dead dry wood must have a significant impact on the availability of nesting sites. The loss of nesting sites is not necessarily accompanied by loss of available provision and will therefore cause a disturbance in the balance of species. The reduction in population size of a predatory wasp may result in a population increase in a prey species. For example a reduction in the population size of the eumenine wasp *Euodynerus euryispilus*, which nests in pre-existing cavities in dead wood, may cause an increase in the population size of its prey caterpillars, the notorious Karoo Caterpillar, *Loxostege frustalis*.

The natural species composition of the riverine vegetation is being seriously altered not only as a result of bush cutting but also by the spread of invasive exotic plant species, most notably mesquites, *Prosopis* species (Mimosaceae), the most aggressive being *P. glandulosa*. The earliest record of the entry of mesquite into southern Africa seems to be its introduction in 1897 to the Okahandja Experimental Garden in Namibia (Harding, 1978). By 1900 it was being cultivated in the Upington area, and since then it has been widely planted in dry areas as a source of fodder. Since mesquite is well adapted to withstand severe droughts it survives in many areas where it can rapidly dominate the less robust indigenous vegetation, forming impenetrable thickets. It is now widespread throughout the Cape Province, Orange Free State and Namibia (Harding and Bate, 1991). All species were declared invader plants in South Africa under the Conservation of Agricultural Resources Act 43 of 1983 and in 1988 two species of bruchid beetles were introduced in an attempt to control its spread, which, however, continues.

The natural species composition of the vegetation and therefore of the associated insects of the stock farming areas is further being disturbed by the establishment of cultivated pastures. These are being increasingly favoured where irrigation or climatic conditions permit. Comprehensive programmes have been set in motion to test all promising pasture crops, whether for inclusion in cultivated pastures or in order to reinforce the natural vegetation. Presently favoured are lucerne, salt-bush (exotic *Atriplex* spp. (Chenopodiaceae)) and spineless cactus (*Opuntia* sp. (Cactaceae)).

As water is required for nesting by excavators in non-friable soil, by builders of aerial mud nests and by those pre-existing cavity nesters which use mud it is relevant to consider available water sources in stock farming areas. Naturally occurring water sources are springs, rivers, temporary pans and temporary rain-water puddles. These are supplemented by man-made earthen dams, contour furrows and water troughs fed from boreholes. In all instances water becomes

unavailable if it is heavily polluted by drinking stock. Only species which alight on the water's surface are able to make use of water sources with steep sides. All those species collecting water or mud at the water's edge require the ground at the water's edge to be gently sloping and not heavily trampled. The impact of stock farming with respect to water on communities of aculeate wasps and bees is variable. Some practices have a negative effect and some a positive effect. Man's actions can cause marked temporary increases or decreases in population size. For example the construction of a small earthen dam in the Clanwilliam district resulted in the growth over a number of years of a large aggregation of thousands of nesting *Ceramius socius* (Masarinae) whereas the subsequent destruction of this dam resulted in a dramatic reduction in the size of this localized population.

Crop farming

Crop production results in a complete change in the available resources. The soil structure and the plant cover of cultivated land are clearly different from those of uncultivated land. Where crops are farmed under irrigation, water sources are modified by changing water flow of rivers and by damming and furrow construction. The impact that cultivation will have on total species diversity clearly depends upon how extensive the cultivation is and how widespread the affected species are.

In those areas where patchy dry land cultivation is practised there is a mosaic of natural communities, cultivated areas in which the vegetation has been replaced by exotics and in which the insects have been in the main excluded by the destruction of their habitats, and fallow land with a small number of pioneer plants and the insects associated with them.

Dry land cropping is mainly practised in the winter rainfall areas, in particular in Namaqualand. To the south of Springbok extensive areas have been ploughed for the opportunistic production of wheat. Replacement of the species-rich vegetation with a single graminaceous species results locally in almost total insect species loss. When such lands are left fallow or abandoned, pioneer plants come in. Initially a limited range of annuals predominate, often forming almost pure stands. These annuals are species which are present but uncommon in the species diverse communities of the surrounding undisturbed areas. An increase in population size of the insect species associated with these plants and a decrease in species diversity as compared with that of the surrounding areas results. This effect is strikingly demonstrated by the wasp and bee species associated with a complex of sympatrically occurring *Wahlenbergia* species (Campanulaceae). A number of species with deep flowers are principally visited by several species of Masarinae, whereas a shallow flowered species *W. annularis* is principally visited by two species of Melittidae. Areas in which the deep flowered *Wahlenbergia* species were formerly abundant and *W. annularis* was uncommon have been cultivated and then allowed to go fallow. In these areas *W. annularis* is now the

dominant plant which has resulted in the masarines being displaced and the melittids having become unnaturally abundant. As on overgrazed land in this area, the first perennial colonizer is *Galenia africana* and this rapidly becomes the dominant species, resulting in a further change in insect representation as discussed above.

In those areas where crops are farmed under irrigation, cultivated land is concentrated on the old flood plains and immediately adjacent areas. As water is available throughout the year, planting time, growing period and success of fertilizer application are not limited by timing and amount of rain. This results in an intensive and continuous use of land for crop production. The use of ever larger multi-span self-propelled overhead sprinklers has resulted in ever larger lands and a consequent continuing loss of unploughed land.

The areas most suited for large-scale cultivation are the same areas which are, due to the availability of water, particularly suited for intensive nesting by a wide range of aculeate wasps and bees. Ploughing, vegetation clearing and replacement with a limited range of crop plants, most of which are exotics, and application of 'artificial out of season rain' results in localized extermination of entire communities. The extent of the cultivated areas and of the distribution ranges of the aculeate wasps and bees will govern the overall extent of this loss. Where there is rapid expansion of land under cultivation and where there is a high incidence of endemism multiple species loss is anticipated. The Olifants River Valley is a notable example of such an area. Five species of *Ceramius* (Masarinae) with limited distributions centred on this area immediately come to mind. One of these five species is *C. metanotalis* which, though it forages on a relatively widespread plant, *Athanasia trifurcata* (Asteraceae), is only known to nest in a limited area on the slopes above the Olifants River between Clanwilliam and Klawer. The area has been ploughed in strips. The forage plants remain on the unploughed strips. The wasps nest on the access road and forage along the strips. Elsewhere along the river, fields are ploughed without strips. Should there be a change to such a ploughing pattern *Ceramius metanotalis* would be endangered.

Aculeate wasps and bees hunt and/or forage beyond the limits of their nesting sites. It is therefore possible to have a situation where, in an intensively cultivated area, suitable nesting sites for some species may remain on the fringes of these areas but their forage and/or prey are no longer available. No masarine wasps and few bees transfer to crop plants. Some megachilid and anthophorid bees are able to forage on exotic leguminous crop plants such as lucerne. It is probable, however, that their foraging distances are such that they cannot make use of flowers in the centres of very large lands (by implication, Bohart, 1972). It does not therefore necessarily follow that the number of individuals which can be supported by a crop plant is in direct ratio to the field size. The limited range of prey insects available on crop plants supports a very limited range of wasps. Crop plants subject to attack by phytophagous insects are generally sprayed with insecticides limiting still further the potential of crops to support these wasps.

Localized large-scale flooding of land resulting from the damming of rivers clearly results in localized extirpation of whole communities of aculeate wasps and bees as a result of total habitat destruction. The availability of water for nesters on the fringes of large water bodies is dependent on the nature of the terrain, inlets with gently sloping shores and still water being more suited to aculeate wasps and bees which collect water or mud than are shores subject to wavelet action. Steep sided water bodies are unavailable to the majority of species. Furthermore, the water in irrigation canals with steep concreted sides and rapidly flowing water is not available to aculeate wasps and bees and therefore such canals do not represent additional water sources for aculeate wasps and bees.

Conservation status

Hilton-Taylor and Le Roux (1989) reviewed the conservation status of the Karoo. They established that of all Acocks's Veld Types of the Karoo Biome (21 occurring in the Nama Karoo and seven in the Succulent Karoo), less than 1% is conserved in all but three types. Six Veld Types have no portions conserved in state, semi-state or private conservation areas. The siting of many reserves in the Karoo has been purely opportunistic or arbitrary, that is without regard to the distribution of endemics and threatened taxa. Furthermore, the areas when declared were already degraded.

Conclusions

Aspects of agricultural land use seen to be adversely affecting the diversity of the aculeate wasp and bee fauna are:

- excessive stocking rates
- heavy selective grazing or browsing
- excessive trampling
- water pollution by stock
- large-scale impoundment of water
- canalizing of water
- extensive replacement of natural vegetation by cultivated pastures
- extensive replacement of natural vegetation by crop plants
- use of insecticides for crop protection
- the spread of invasive exotic plant species
- bush cutting
- intensive removal of dry wood.

The nature and extent of agricultural land use in the semi-arid areas of southern Africa, the Karoo, is such that there are already no truly pristine areas extant. The number of areas suited to supporting the present typical aculeate wasp and bee communities is increasingly on the decline. As aculeate wasps and

bees show a high level of beta diversity, being habitat specialists, they are not adaptable to change. Consequently over much of the area alpha diversity has already been reduced. Continued and increasing exploitation is expected to result in total loss at least of endemic species. Greatest species loss is expected in the Succulent Karoo as this is an area rich in species showing high levels of delta rarity, that is rich in endemics, both floral and faunal.

Due to their interaction with plants, other insects and spiders, disturbances in abundance and species representation of aculeate wasps and bees will have a cascade effect which will inevitably affect the whole ecological system of the Karoo.

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Comparison of the Arboreal Ant Mosaic in Ghana, Brazil, Papua New Guinea and Australia – its Structure and Influence on Arthropod Diversity

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Introduction

Throughout the subtropical and tropical regions of the world, ants have been reported as comprising a major component of rain forest and tree crop canopy faunas. Examples of such observations include those of: Fittkau and Klinge (1973), Leston (1978), Erwin (1983) and Adis *et al.* (1984) for Brazil; Erwin (1985) and Wilson (1987) for Peru; Room (1971) and Leston (1973) for Ghana, West Africa; Way (1954a,b) for Tanzania, East Africa; Stork (1987) for Borneo, South-east Asia; and Majer (1990) for Australia.

Fittkau and Klinge (1973) estimated that ants constitute nearly one-third of the arboreal arthropod biomass in Brazilian rain forest and this figure was confirmed by Adis *et al.* (1984) (29% of total arthropod biomass, or 51% of total numbers). Leston (1973), quoting data in Majer (1973), indicated that in the Ghanaian cocoa fauna, 89% of the specimens were ants, while in Borneo, Stork (1987) showed that ants comprised 18% of individuals in the arthropod tree fauna. The species richness of arboreal ants in the tropics mirrors their high abundance; for instance, Room (1971) sampled 67 species of ants from cocoa canopy in Ghana, Wilson (1959) found 56 species of ants in approximately 5 km² of New Guinea rain forest canopy, Room (1975a) found 88 species of ants in hand and knockdown samples of cocoa canopy in Papua New Guinea, while Wilson (1987) found 135 species in the canopy of a comparable area of Peruvian

rain forest. When ants from other strata are included, the richness of the fauna is even greater, for instance Verhaagh (1990) found over 500 ant species in a 10 km² area of Peruvian rain forest, Cover *et al.* (1990) sampled 256 species along four 20×500 m transects through Peruvian forest, and Room (1971) found an overall total of 128 species in the 250 m² cocoa farm which he surveyed.

Of the ants found within the canopy, a few species tend to dominate numerically the remainder of the ant fauna. Based on observations in West Africa, Room (1971), Majer (1972) and Leston (1973) nominated these species as dominant ants because of their numerical superiority and their tendency to exclude other dominant species from their territory. In both the New and Old World tropics, these dominant ants have been reported to be distributed in a mosaic-like pattern within tree crop plantations (see review by Jackson, 1984). This three-dimensional patchwork of non-overlapping dominant species is thought to arise from competitive interactions and also by their differing micro-habitat requirements (Leston, 1973).

In view of the ubiquity, abundance and diversity of ants in tropical areas, it is not surprising that ants participate in significant interactions with other components of the community. Table 5.1 lists some of the reported interactions from Ghana and Brazil, and reveals that they occur between members of the fungi, plant and animal kingdoms. Perusal of the literature indicates that the participants in these interactions are often confined to certain fungi, plant or animal species with individual subfamilies, genera or species of ant. Thus the ant community possesses the capacity to influence the occurrence of these components of the community.

Frequently, but not always (see Way *et al.*, 1989), it is the dominant ant which plays the major role in the interactions with other components of the community. As a result of this, considerable attention has been focused on the role of the mosaic of dominant ants in the distribution and limitation of certain pests or pathogens within tree crops (Leston, 1973; Room, 1974; Majer, 1986; Way and Khoo, 1992). Working from the theoretical point of view, Gilbert (1990) regarded the ant mosaic as one of the four major biotic organizational features which mould the species composition and diversity of the biota in neotropical forests. This, he believes, is by ants controlling the rates of herbivory on plants, which in turn results in a degree of patchiness in the forest. The other major biotic features which mould the neotropical forest community are:

1. the existence of a *chemical mosaic* of different plant species which in turn possess their own co-evolved food webs;
2. the animals which form the *mobile links* between different plant species as a result of their role in reproduction and dispersal of plant propagules;
3. the *keystone mutualist* plant species which support link organisms and thus indirectly support those food webs which depend upon mobile links for all or part of their species richness (Gilbert, 1980).

From what I have said, it seems that the ant mosaic should have a major

Table 5.1. Examples from Ghana or Brazil in which the arboreal ant fauna can locally influence some components of the biological community.

Interaction with	Type of interaction	Reference
Entomogenous fungi in Ghana	Many species of fungi infect ants and often have a restricted host range at the generic or tribal level	Evans (1982)
Nectaries of flowering plants in Brazil	Many ant species attend extra-floral nectaries and confer some protection to plants; attendance is confined to certain subfamilies of ants	Oliveira and Brandão (1989)
Epiphytic plants in Brazil	Nests of certain ant species support 'gardens' of a wide range of epiphytic plants as a result of their dispersing seeds into nests	Mann (1912)
Canopy arthropod fauna in Ghana	The differing rates of predation by, and feeding preferences of, various dominant ants affect the composition of the canopy fauna	Majer (1976c)
Sap-producing Homoptera in Ghana	Many ant species tend aphids, coccids or other Homoptera and these mutualistic interactions are sometimes restricted to individual species or genera	Leston (1970)
Non-dominant ants in Ghana	As a result of their differing degrees of specialization, each species of dominant ant has different species of non-dominant ant associated with it	Room (1971)

Table 5.2. Comparison of arboreal dominant ants in tree crop plantations or native vegetation in the four continents which contain countries with tropical or subtropical climates.

Country and plant community	Ant species	Sub-family*	Dominance status**	Reference
Central and South America				
Brazil – subtropical forest (7)*	<i>Azteca bicolor</i>	D	D	Leston (1978)
	<i>Azteca paraensis</i>	D	D	
	<i>Cephalotes atratus</i>	M	SD	
	<i>Crematogaster acuta</i>	M	D	
	<i>Dolichoderus attelaboides</i>	D	D	
	<i>Ectatomma tuberculatum</i>	P	D	
	<i>Hypoclinea bidens</i>	D	D	
Brazil – cocoa plantation (2, 3, 4, 6)	<i>Azteca chartifex spiriti</i>	D	D	Majer and Delabie (unpublished)
	<i>Azteca</i> sp. 11	D	D	
	<i>Cephalotes atratus</i>	M	SD	
	<i>Crematogaster acuta</i>	M	D	
	<i>Crematogaster erecta</i>	M	D	
	<i>Crematogaster limata</i>	M	D	
	<i>Ectatomma tuberculatum</i>	P	D	
<i>Wasmannia auropunctata</i>	M	D		
Venezuela – cocoa plantation (7)	<i>Azteca forelli</i>	D	D	Jaffe <i>et al.</i> (1986 and pers. comm.)
	<i>Cephalotes atratus</i>	M	D	
	<i>Crematogaster</i> spp.	M	D	
	<i>Monacis bispinosus</i>	D	D	
	<i>Solenopsis</i> spp.	M	D	
Trinidad – cocoa/ coconut, coffee/ citrus plantations (?)	<i>Azteca</i> sp. 1	D	D	Way (pers. comm.)
	<i>Azteca</i> sp. 2	D	D	
	<i>Wasmannia auropunctata</i>	M	D	
Costa Rica – cocoa plantation (?)	<i>Crematogaster limata palens</i>	M	D	Young (1986 and pers. comm.)
	<i>Paratrechina longicornis</i>	F	D	
	<i>Solenopsis tenuis</i>	M	D	
	<i>Wasmannia auropunctata</i>	M	D	
Africa				
Ghana – cocoa plantation (<)	<i>Camponotus acvapimensis</i>	F	SD	Majer (1972)
	<i>Crematogaster buchneri</i>	M	D	
	<i>Crematogaster castanea</i>	M	SD	
	<i>Crematogaster clariventris</i>	M	D	
	<i>Crematogaster depressa</i>	M	D	
	<i>Crematogaster kneri</i>	M	SD	
	<i>Crematogaster striatula</i>	M	D	
	<i>Oecophylla longinoda</i>	F	D	
	<i>Platythyrea frontalis</i>	P	SD	
	<i>Tetramorium aculeatum</i>	M	D	
Nigeria – cocoa plantation (3, 6, 6)	<i>Acantholepis capensis</i>	F	SD?	Taylor (1977)
	<i>Acantholepis</i> sp. T2	F	SD?	
	<i>Crematogaster africana</i>	M	D	
	<i>Crematogaster clariventris</i>	M	D	

Country and plant community	Ant species	Sub-family*	Dominance status**	Reference
	<i>Crematogaster depressa</i>	M	D	
	<i>Oecophylla longinoda</i>	F	D	
	<i>Pheidole megacephala</i>	M	SD?	
	<i>Tetramorium aculeatum</i>	M	D	
Cameroon – cocoa plantation (2, 3)	<i>Crematogaster africana</i>	M	D	Jackson (1984),
	<i>Crematogaster gabonensis</i>	M	D	Bruneau de Miré (1969)
	<i>Oecophylla longinoda</i>	F	D	
	<i>Tetramorium aculeatum</i>	M	D	
	° <i>Wasmannia auropunctata</i>	M	D	
Tanzania – coconut plantation (2, 3)	<i>Anoplolepis custodiens</i>	F	D	Way (1953),
	° <i>Anoplolepis longipes</i>	F	D	Vanderplank (1960)
	<i>Crematogaster castanea</i>	M	SD?	
	<i>Crematogaster rectinota</i>	M	SD?	
	<i>Oecophylla longinoda</i>	F	D	
	<i>Pheidole megacephala</i>	M	D	
	<i>Pheidole punctulata</i>	M	D	
Asia				
Sri Lanka – coconut plantation (3)	<i>Crematogaster</i> sp.	M	D	Way <i>et al.</i> (1989)
	° <i>Paratrechina longicornis</i>	F	SD	
	<i>Oecophylla smaragdina</i>	F	D	
Solomon Islands – coconut plantation (3)	° <i>Anoplolepis longipes</i>	F	D	Greenslade (1971),
	<i>Iridomyrmex cordatus</i>	D	D	Macfarlane (1985)
	<i>Oecophylla smaragdina</i>	F	D	
	° <i>Pheidole megacephala</i>	M	D	
	° <i>Wasmannia auropunctata</i>	M	D	
Malaysia – cocoa/coconut plantations (?)	° <i>Anoplolepis longipes</i>	F	D	Way and Khoo (1989, 1991), Way (pers. comm.)
	<i>Dolichoderus thoracicus</i>	D	D	
	<i>Dolichoderus</i> sp. nr. <i>gibbus</i>	D	D	
	<i>Oecophylla smaragdina</i>	F	D	
	<i>Pheidole ferrens</i>	M	D	
	<i>Iridomyrmex cordatus</i>	D	D	
Indonesia – cocoa plantation (?)	° <i>Anoplolepis longipes</i>	F	D	Giesberger (1983)
	<i>Dolichoderus thoracicus</i>	D	D	
	<i>Oecophylla smaragdina</i>	F	D	
Papua New Guinea – cocoa plantation (?)	° <i>Anoplolepis longipes</i>	F	D	Room (1975a)
	<i>Crematogaster</i> sp. R114	M	D	
	<i>Oecophylla smaragdina</i>	F	D	
	° <i>Technomyrmex albipes</i>	F	D	
Australasia				
Australia – mango (2)	<i>Oecophylla smaragdina</i>	F	D	Majer and Camer-Pesci (1991)
	<i>Crematogaster</i> sp.	M	SD?	

*D = Dolichoderinae, F = Formicinae, M = Myrmicinae, P = Ponerinae.

**D = Dominant, SD = Sub-Dominant or Co-Dominant.

° = Tramp species which have probably been introduced to region.

* = Numbers of species of dominant ant in plots which were surveyed.

impact on the biodiversity of the community in which it occurs. This chapter therefore has the following aims:

1. It first reviews the small-scale distribution of arboreal ants throughout the tropics to see whether the ant mosaic is a universal phenomenon.
2. It describes and compares the ant mosaic in Ghana, Brazil, Papua New Guinea and Australia in areas where comparable survey techniques have been performed.
3. It compares the number of dominant ants which comprise the mosaic in the four areas.
4. It examines the impact of the mosaic on the distribution and species diversity of non-dominant ants.
5. It examines the impact of the mosaic on the distribution, species composition and, ultimately, the species diversity of other invertebrate groups which occupy the canopy.

How Widespread is the Ant Mosaic?

Table 5.2 shows examples of studies in which dominant ants, if present, have been mapped in the canopy of forests or tree crops. Studies which have deliberately focused on individual ant species are not included in this table. In some cases, a species of ant is numerous in the canopy but co-exists with another dominant or only reaches high population densities under exceptional circumstances (e.g. a break in the canopy or an area where none of the major dominants is present); these are collectively referred to as sub-dominants in Table 5.2. This table indicates that dominant ants, and the associated mosaics, exist throughout Central and South America, Africa, Asia and into northern Australia.

In some cases, introduced tramp species such as *Anoplolepis longipes*, *Anoplolepis custodiens*, *Paratrechina longicornis*, *Technomyrmex albipes* or *Pheidole megacephala* make up significant components of the mosaic. However, most components of the mosaic are native species. In the Americas, the mosaic comprises members of the Dolichoderinae (in particular *Azteca* spp.), Myrmicinae and, to a lesser extent, Ponerinae. The profile of subfamilies in Africa is similar except that the Dolichoderinae are replaced by the Formicinae and the Ponerinae are of little importance, while in Asia the mosaics consist of members of the Formicinae, Myrmicinae and Dolichoderinae. The ground-nesting dolichoderine, *Iridomyrmex cordatus*, contributes to the mosaic in Malaysia and the Solomon Islands and, although not featuring in any publications where ants have been mapped, other dolichoderines, *Dolichoderus* spp., reach dominant status in South-east Asia (Van der Goot, 1917; Way and Khoo, 1989; Way, pers. comm.). The variety of dominants in northern Australia is much less, with *Oecophylla smaragdina* (Formicinae) and, arguably, *Crematogaster* sp. (Myrmicinae) reaching dominant status. Only one genus, *Crematogaster*, consistently features

as a native dominant within mosaics in all of the four continents which feature tropical or subtropical climates.

Most of the mosaics described in Table 5.2 pertain to tree crop situations. However, Leston's (1978) data are largely from subtropical rain forest in Brazil and his (1973) publication features data on dominant ants in secondary rain forest in Ghana. Furthermore, Hölldobler (1979, 1983) has respectively produced maps of *Oecophylla* spp. colonies in Kenyan forest and cleared rain forest in Queensland, Australia. It therefore appears that the mosaic is a feature of native, as well as agroecosystems, although the vertical separation of the blocks of the mosaic is considerably more pronounced in the former.

Comparison of ant mosaics in different regions is confounded by the different sampling techniques and areas which have been mapped by the various workers. Inspection of Table 5.2 does, however, indicate that the number of dominant ant species which comprise the mosaic is lowest in Australia and also is lower in Asia than it is in Africa or the Americas. In the following section, four mosaics are compared in areas where comparable survey techniques have been used.

Ant Mosaics in Ghana, Brazil, Papua New Guinea and Australia

Methods

The majority of the data for Ghana are from Leston (1973), Majer (1972, 1973, 1976a,b,c) and Room (1971); for Brazil from Majer and Delabie (unpublished); for Papua New Guinea from Room (1975a,b) and Room and Smith (1975); and for Australia from Majer and Camer-Pesci (1991).

Plots of cocoa in Ghana and Brazil and mango in Australia were selected for mapping of ants. (Ants were not mapped in Papua New Guinea.) Each tree was inspected for a period of 5 min, and the ants which foraged on the trunk or leaves were collected for later identification. The canopy of tall trees was inspected with the aid of binoculars. The nesting habit of each species was recorded and a subjective assessment of the general abundance of each species on trees was noted. Unless otherwise stated, if more than 200 ants could be seen and individuals were present on much of the tree, the ant was regarded as dominant.

In order to assess the relationship between the distribution of dominant and non-dominant ants, the entire ant community was assessed on a large sample of individual cocoa trees in Ghana (Room, 1971), Brazil (Majer and Delabie, unpublished) and Papua New Guinea (Room, 1975a). Ants were hand collected on trees for a period of 5 min. (Ants were not surveyed in this way in Australia.)

Ants and other invertebrates were further quantified by the chemical knock-down technique. Prior to sampling, the undergrowth was slashed in order to facilitate the placing of sheets of calico beneath the canopy (25 m² sheets used in Ghana and Australia, 16 m² sheets used in Brazil, 9 m² used in Papua New

Guinea; all data corrected to 25 m² area). On the following day the canopy was sprayed with a rapid-knockdown pesticide using a motorized knapsack mistblower with a vertical throw of about 10 m. After 30 min, the canopy was shaken to dislodge dead or dying animals and these were transferred from the sheets to vials of 70% alcohol. The animals were sorted to at least order or family level (species level in Ghana and partly to species level in Papua New Guinea) and the specimens were then drained for 12 h in filter paper funnels. The resulting weight of the sample was considered to be an estimate of live weight of the animals in the < 10 m canopy stratum.

Results

Samples of dominant ant distribution patterns are shown in Figs 5.1, 5.2 and 5.3 for comparable areas of tree crop in Ghana, Brazil and Australia respectively. The

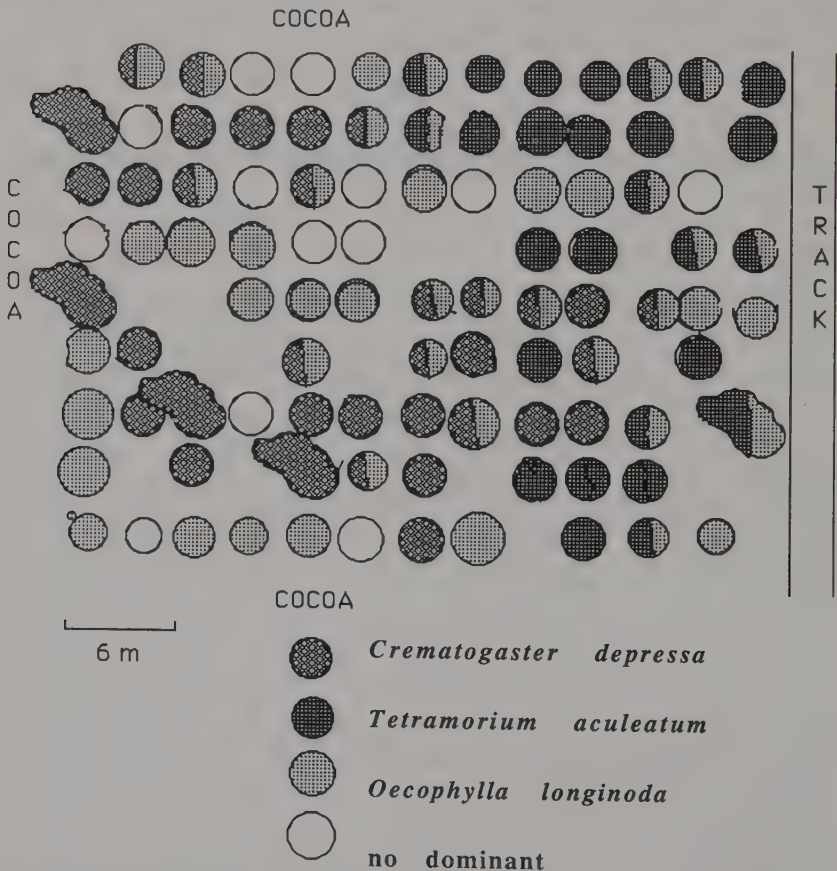
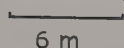


Fig. 5.1. Example of dominant arboreal ant distribution on cocoa trees at Kade, Ghana (adapted from Majer, 1976a).



distribution patterns of ants in Ghana and Brazil are relatively similar in that they form a reasonably densely-packed mosaic of ants, with colonies of each dominant ant species occupying several contiguous trees and with few trees lacking dominant ants. The more extensive surveys reported in Majer (1972, 1976a) indicate at least 70% occupancy of the Ghanaian cocoa trees by dominant ants

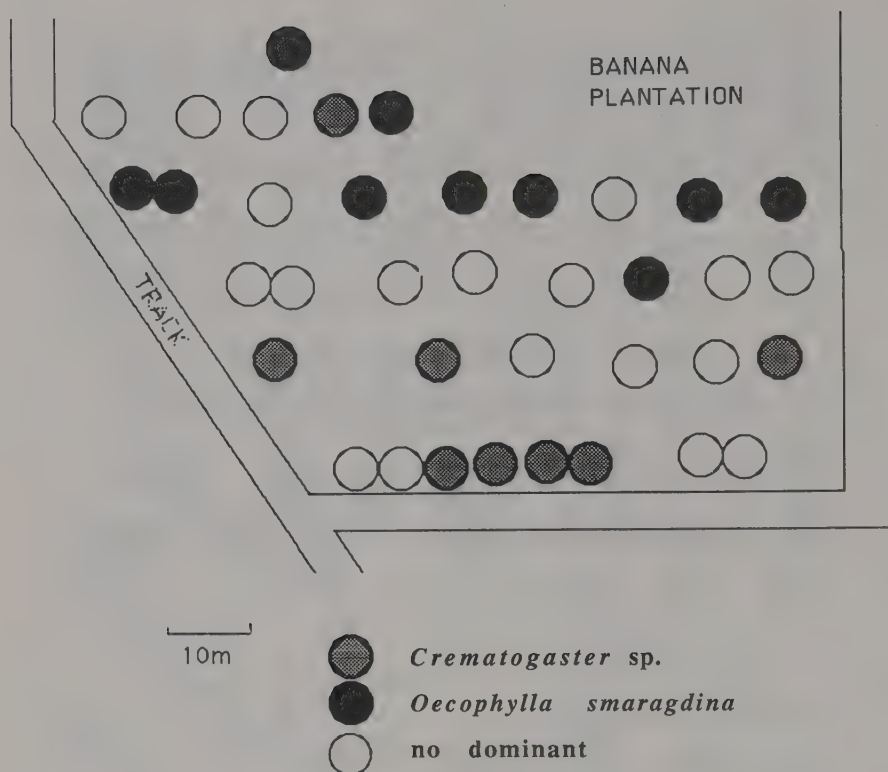


Fig. 5.3. Example of dominant arboreal ant distribution on mango trees at Kununurra, Australia. In terms of abundance, *Crematogaster* sp. is probably a sub-dominant rather than dominant ant (adapted from Majer and Camer-Pesci, 1991).

and for Brazil 90–97% occupancy (Majer and Delabie, unpublished). The latter study revealed one exception, an area of old, densely shaded cocoa trees which had not been sprayed with insecticide for many years and which supported dominant ants on only 24% of the trees. The Australian plantation (Fig. 5.3), and others reported in Majer and Camer-Pesci (1991), differed in that many more trees were devoid of dominant ants. These trees were foraged on by a range of species of ground-nesting ants which did not necessarily utilize contiguous trees and therefore did not exhibit a pronounced mosaic pattern.

The 30×40 m areas of cocoa which were mapped in Brazil supported 2–6 species of dominant ants each, which is comparable with the range of dominant species in similar areas of cocoa in Ghana. As already mentioned, only one (*O. smaragdina*), or perhaps two (*Crematogaster* sp.), ant species dominated the mango in Australia. The cumulative checklist of dominant ants in the Brazilian

and Ghanaian cocoa (respectively eight and ten species) and Australian mango (one or two species) broadly reflected the trend in number of dominant species in individual plots. With a total of four dominant species, Papua New Guinea is intermediate between the Australian and Brazilian totals (Table 5.2).

Influence of the mosaic on non-dominant ants

Figure 5.4 shows the mean number of various species of dominant ants in 25 m² chemical knockdown sample equivalents taken in Ghana, Brazil and Australia (no data are available for Papua New Guinea). *Oecophylla longinoda*, *Tetramorium aculeatum* and *Crematogaster striatula* in Ghana and *O. smaragdina* in Australia were all extremely abundant, being taken in excess of 1000 individuals per sample. By contrast, the numbers of dominants on the Brazilian trees were considerably lower, with numbers ranging within the hundreds for *Azteca* spp. and *Crematogaster erecta*. The low numbers of *Wasmannia auropunctata* are probably caused by the ant nesting at ground level and hence not being adequately sampled; very high densities are often observed attending *Coccoidea* on cocoa pods. The density of *Ectatomma tuberculatum* was genuinely low; I would still classify it as a dominant ant in view of its aggressive behaviour and its

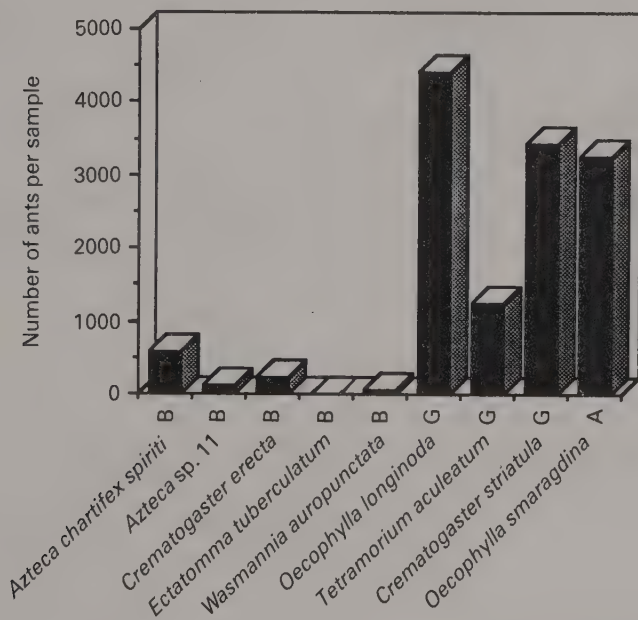


Fig. 5.4. Numbers of dominant ants in 25 m² chemical knockdown samples of cocoa in Brazil (B) and Ghana (G) and of mango in Australia (A) (data are taken from Majer and Delabie (unpublished) for Brazil, from Majer (1973) for Ghana, and from Majer and Camer-Pesci (1991) for Australia).

(b)

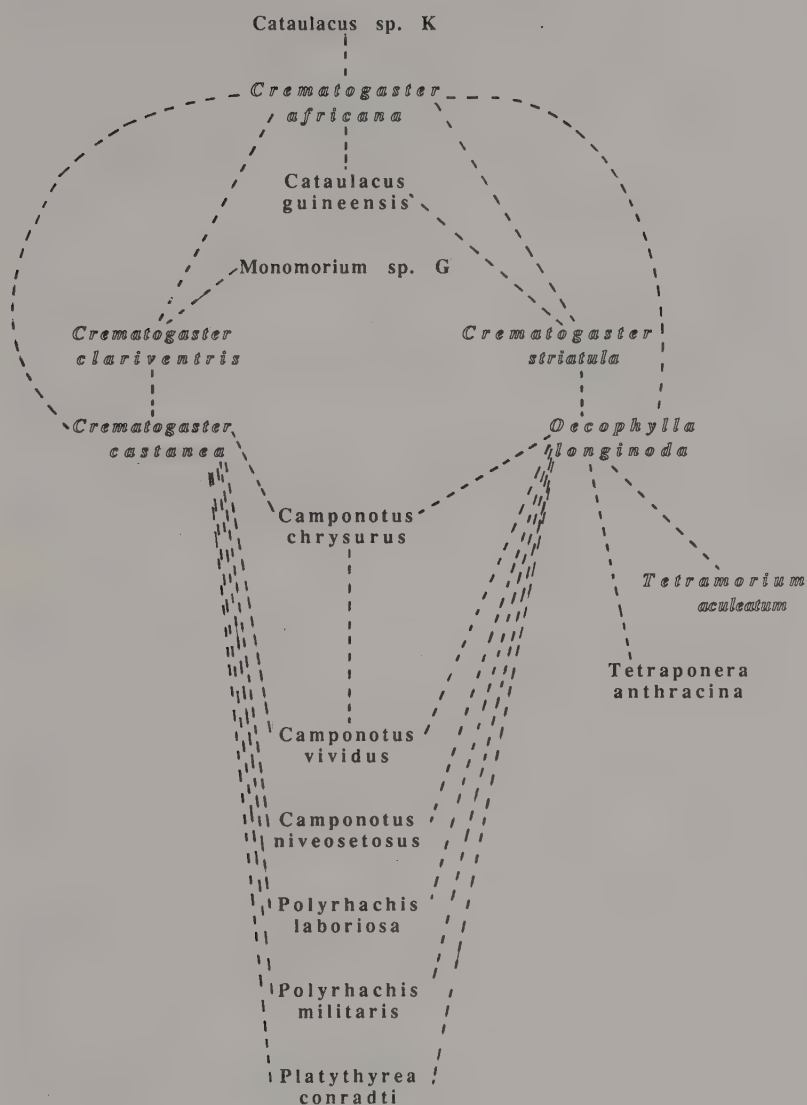


Fig. 5.5. continued. See legend opposite.

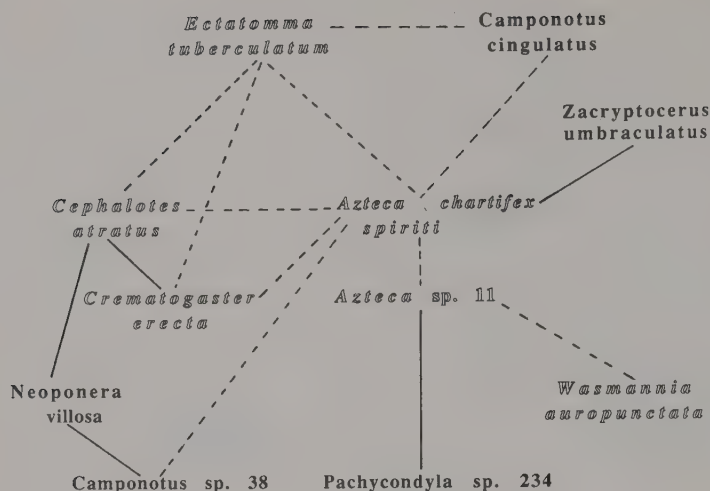


Fig. 5.6. Positive (solid lines) and negative (broken lines) associations ($p < 0.05$ using Fisher's exact test) between the various ant species in a cocoa farm at Itabuna, Brazil. The dominant and sub-dominant species are shown in *italics* (adapted from Majer and Delabie, unpublished).

ability to monopolize large tracts of canopy to the exclusion of other dominants (Majer and Delabie, unpublished).

In view of the predominance and/or aggressiveness of these ants, it is not surprising that the species composition of the associated dominant ants is affected. Room (1971) performed a chi square association analysis for the 36 ant species which were commonly found on 168 cocoa trees which he sampled in Ghana. Figures 5.5(a) and (b) respectively show the positive and negative associations observed between the various ant species. No direct positive, but several negative associations were observed between dominant ant species, thus confirming their mutual exclusivity. Figure 5.5(a) indicates that each dominant appears to have its own sub-community of non-dominant ants with which it is able to co-exist and that there is little overlap in the species composition of these various sub-communities.

Figure 5.6 shows the significant positive and negative associations between dominant or sub-dominant ants on the 107 Brazilian cocoa trees mapped in Fig. 5.2. The use of this statistical procedure is not, strictly speaking, valid because neighbouring trees were used in the analysis; it does, however, give some indication of the sorts of relationships that exist between the ant species. Once again, the negative association between dominant species was apparent. Three non-dominant ants exhibited positive associations with certain dominant species. The lower number of positive associations than Room (1971) observed is probably

caused by the lower number of trees surveyed and also because the analysis was performed on contiguous trees, which would undoubtedly support a more restricted range of ant species. However, using pyrethrum knockdown data from a wider range of trees, Majer and Delabie (unpublished) found that there was a statistically significant tendency for ants of a similar length to the dominant to be absent from the territory of that species. It therefore seems that, as in Ghana, the Brazilian dominants have a tendency to influence the species composition of the non-dominant ants, with which they are associated.

The significant positive and negative associations between hand-collected ants in the Papua New Guinea cocoa are shown in Figs 5.7(a) and (b) respectively. Once again, mutual exclusivity between most combinations of dominant ants (*A. longipes*, *Crematogaster* sp. R114, *O. smaragdina* and *T. albipes*) was observed, confirming that these ants were also distributed in a mosaic-like fashion (Fig. 5.7(b)). As in the previous two locations, various non-dominant species were associated with the dominant and Fig. 5.7(a) indicates a possibility of even more species if pyrethrum knockdown rather than hand collection data are analysed (see Room, 1975a).

It was not possible to perform a similar analysis on the Australian mango trees in view of the rather low number of sampling units. However, application of Fisher's exact test indicated negative associations between *O. smaragdina* and *Crematogaster* sp. and also between *Crematogaster* sp. and *P. longicornis*.

It therefore seems that the sub-dominant ant fauna of the canopy is patchily distributed, with sub-communities of non-dominant ants reflecting the distribution of the mosaic of dominant ants. In addition to variations in species composition, there are also variations in the number of species co-existing with the various dominant species. This has been observed in Ghana (*C. striatula* had the fewest species associated with it, *Crematogaster clariventris* the most), Brazil (*Azteca chartifex spiriti* and *E. tuberculatum* had the fewest associated species, *Azteca* sp. 11 the most), and also in Papua New Guinea (*T. albipes* had the fewest associated species, *O. smaragdina* the most).

Impact of the mosaic on other invertebrates

In addition to their numerical predominance among the overall ant fauna, the dominant ants also contribute greatly to the total invertebrate biomass on the trees. Figures 5.8(a), (b) and (c) show the biomass of certain dominant ants, for which there are data, and the associated invertebrates on the Ghanaian, Brazilian and Australian trees respectively. In both Ghana and Australia, *Oecophylla* spp. contribute over three-quarters of the invertebrate biomass on trees. The contribution by other ants is lower but not inconsiderable, ranging from 5 to 12% in Ghana and 10 to 31% in Brazil.

Therefore, in view of their high contribution to biomass, it might be expected that dominant ants may profoundly influence the abundance and composition of the associated fauna. This has not yet been investigated in

(a)

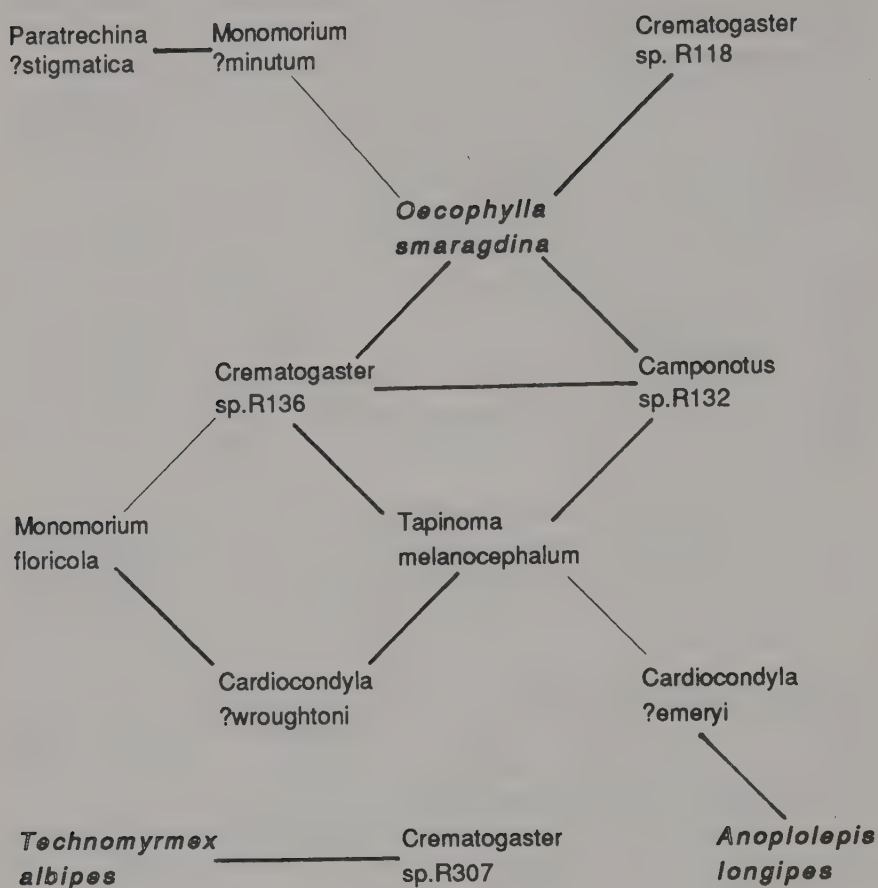


Fig. 5.7. (a) Positive (solid lines) and (b) negative (broken lines) associations (thick lines $p < 0.05$, thin lines $p < 0.1$ using chi square analysis) between the various ant species in cocoa farms in Papua New Guinea. The dominant species are shown in italics (adapted from Room, 1975b).

northern Australia but in Ghana, Majer (1976c) took 144 chemical knockdown samples from territories of different dominants and examined the composition of the fauna by principal components analysis ordination. Using 100 invertebrate species as descriptors of the sample, it was found that the samples separated out on axes 2 and 3 of the ordination on the basis of which species of ant dominated the sample. Furthermore, samples in which the dominant ant was particularly abundant were more extremely separated than those with lower ant densities.

(b)

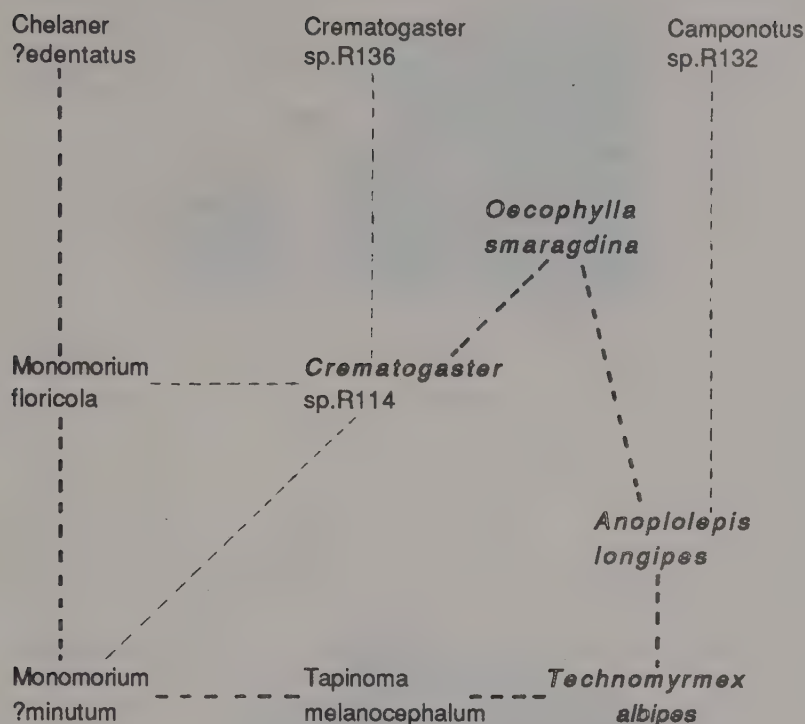


Fig. 5.7. *continued.* See legend opposite.

Thus each dominant ant had a characteristic invertebrate fauna, which became even more distinctive at high ant densities.

This separation of fauna on the basis of the dominant ant was further confirmed by performing an ordination of the 100 most common invertebrate species, using the samples in which they occurred as their descriptive attributes. The dominant ants were well separated on the second and third axes of the ordination, once again illustrating their mutual exclusivity. 'Clouds' of associated invertebrates were distributed in the region of each dominant ant, although the number of associated species varied according to the ant species. *O. longinoda* was associated with the lowest number of taxa, *C. striatula* with the most, and *T. aculeatum* exhibited intermediate numbers of associated invertebrates.

As part of Majer's (1976c) study, selected dominant ants were mechanically removed from certain plots. In time, the resulting lacunae which were created in the mosaic were generally filled by the lateral spread of adjacent dominant ants. Inclusion of the newly colonized areas in the ordination analysis indicated that the invertebrates in the samples were more closely allied with the ant which had

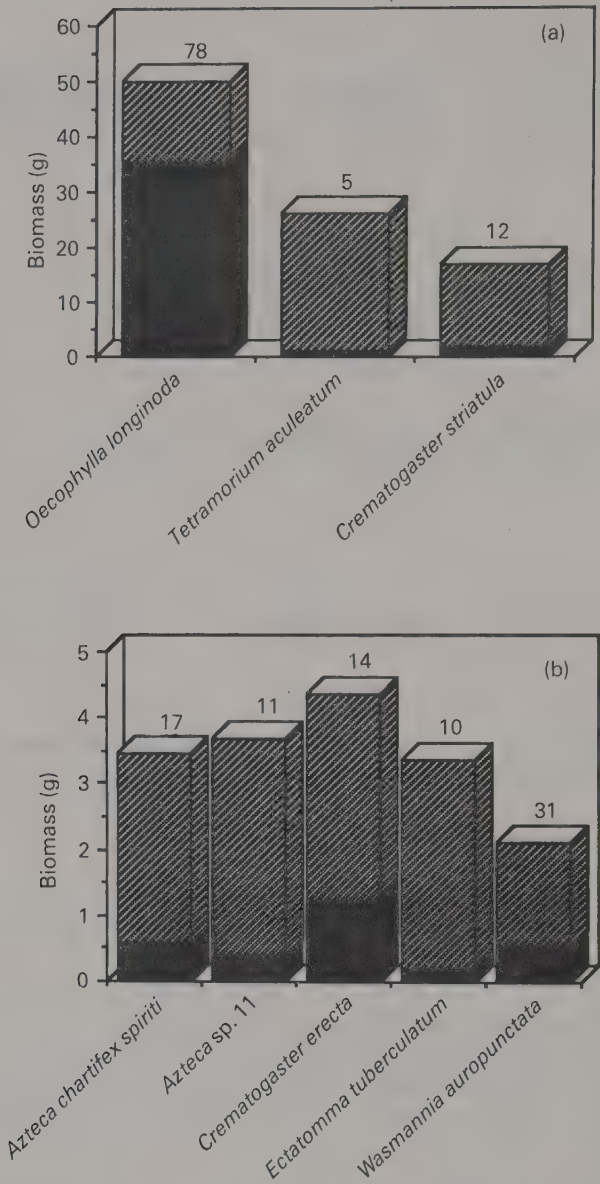


Fig. 5.8. Biomass of dominant ants (solid) and other invertebrates (hatched) in 25 m² chemical knockdown samples of cocoa in (a) Ghana and (b) Brazil and mango in (c) Australia (opposite). Numbers above the histograms show the percentage contribution of dominant ants to total invertebrate biomass (data are taken from the same sources as for Fig. 5.4).

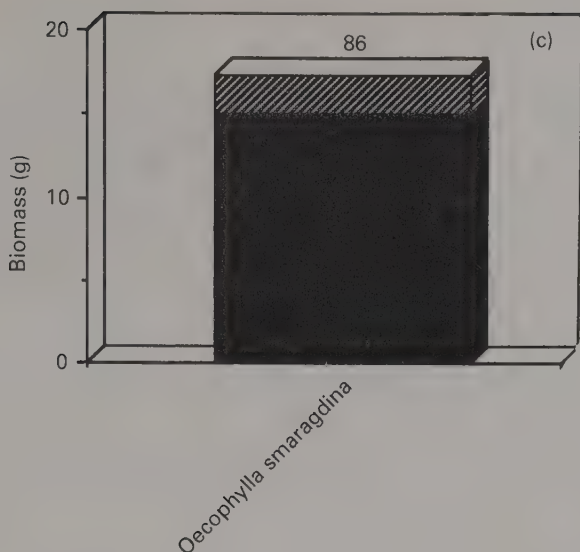


Fig. 5.8. continued. See legend opposite.

colonized the area than with the one which had been eliminated. It therefore appears that deliberate alteration of the ant fauna can bring about changes in the composition of the associated invertebrates.

It is not possible to discuss the impact of the Brazilian dominant ants on the invertebrate fauna because the chemical knockdown data have not been sorted to species level. However, at the order level, significantly lower numbers of individuals were encountered within *A. chartifex spiriti* territory than within those of the other dominants mentioned in Fig. 5.8(b) (e.g. Blattodea, Mantodea, Orthoptera, Hemiptera and Neuroptera) while the large ponerine *E. tuberculatum* tended to be associated with significantly lower numbers of those taxa which contained larger insects (e.g. Blattodea, Mantodea and some Diptera). It is probable that these differences in invertebrate abundance extend to differences in the diversity and species composition of the invertebrate fauna.

The relationships between certain pest species, certain environmental parameters and some of the most frequently occurring ant species in the Papua New Guinea knockdown samples were analysed by chi square analysis. Both *A. longipes* and *O. smaragdina* were found to be negatively associated with a range of insect species, although a range of positive and negative associations between certain ant species and environmental components was also observed (Room and Smith, 1975). Some of the negative associations between ants and other insects represented direct biological relationships (e.g. harassment of the curculionid *Pantorhytes szentivanyi* by *A. longipes*), while other ant-insect relationships were indirect as a result of their exhibiting similar responses to particular habitat components.

Discussion

This review has indicated that the arboreal ant mosaic is a widespread phenomenon throughout the New and Old World tropics and that it exists both in tree-crop plantations and within native vegetation. Although the mosaic is well defined and densely packed in the tropical parts of Africa, Asia and America, there are many lacunae in the northern Australian mosaic. It appears that the ant mosaic becomes less common or non-existent as one moves away from the tropics; Majer and Queiroz (1989), for instance, did not detect a mosaic in coffee at Viçosa, Minas Gerais, which is several hundred kilometres further south than the Brazilian cocoa plantation described in this chapter. This could be due to an absence of arboreal ant species which are capable of producing colonies of high density or it could result from limitations to secondary productivity within that area. The subsequent low energy flux within the canopy might be insufficient to allow the differentiation of a patchwork of territories of different dominants which are able to exploit combinations of prey species in different ways in the various blocks of the mosaic (Room, 1971).

The mapping of individual colonies of dominants (e.g. Majer, 1976a; Hölldobler, 1979, 1983) indicates that while some colonies are small and localized, individual colonies of certain dominants can cover several hundred square metres of canopy. Furthermore, extended studies on the distribution of dominants (e.g. Greenslade, 1971; Majer, 1976b) have indicated that within the medium-term time span (several months to a year or so), the mosaic is relatively stable. Thus the mosaic has the potential to mould the community within its blocks at both the short-term ecological or even the long-term evolutionary level.

In the Ghanaian, Brazilian and New Guinean examples reviewed here, the dominant ants are found to have a marked influence on the distribution of non-dominant ants. Indeed, it appears that separate sub-communities of non-dominant ants characterize the territories of each dominant species, the composition of which reflects those species which are able to co-exist without competing with the dominant (Room, 1971, 1975a). The actual number of ant species which may co-exist with the dominant may reflect the degree of specialization of the latter; a more specialized species would tend to have more species associated with it, while one with a broader niche would overlap the requirements of a greater number of species and hence be associated with fewer species (Room, 1975a). As a result of the dominant/non-dominant ant relationship, the mosaic could have the effect of increasing ant diversity through the structuring of a range of different sub-communities of non-dominant ants within the mosaic of dominants. Although it has not yet been investigated, I consider that the diversity of non-dominant arboreal ants in northern Australia may be lower than in areas where a well-defined mosaic exists. This may be because the extensive lacunae which exist there are intermittently foraged by a wide range of ground-nesting ants (Majer and Camer-Pesci, 1991). The continual change in visitation by different species of ants, which reflects the constantly changing patterns of

foraging trails on the ground, would mitigate against the development of sub-communities of ants which are able to co-exist with a particular dominant; only in the territory of *O. smaragdina* or perhaps the lower density *Crematogaster* sp., would a non-dominant ant fauna have the opportunity to become assorted on the basis of a continuously present dominant ant.

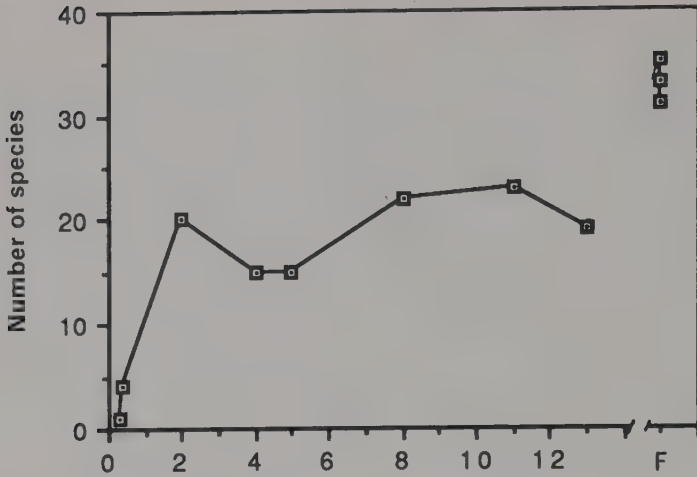
The mosaics are largely composed of native ant species (Table 5.2). In some areas the mosaic is also contributed to by cosmopolitan tramp species, which have been deliberately or accidentally introduced into the area. Generally speaking, these are generalist species which can nest under a broad range of habitat regimes and feed on a wide variety of food sources. There are many reports on the impact of introductions of dominants such as the Argentine ant, *Iridomyrmex humilis*, and *Pheidole megacephala* on the ant fauna in general (e.g. Haskins and Haskins, 1965; Fluker and Beardsley, 1970), but little has been recorded on the impact of these species on ant diversity. Majer and de Kock (1992) observed the succession of ants in rehabilitated sand mines at Richards Bay, South Africa. This is in an area of subtropical coastal dune forest which has a moderately abundant arboreal ant fauna, characterized by the dominants *T. albipes* and *Crematogaster* spp. on trees. Despite an initially rapid increase in the number of ant species from all strata, there was a slight decline in ant species during years 2–5 of the succession (Fig. 5.9(a)). This coincided with a massive build-up in the density of *P. megacephala* and was followed by a second increase in diversity when *P. megacephala* commenced to decline after the fifth year of rehabilitation (Fig. 5.9(b)). It was only by year 13, when *P. megacephala* ceased to dominate the trees, that *T. albipes* and *Crematogaster* spp. started to colonize the trees in large numbers. From these observations, it appears that the arrival of a cosmopolitan tramp species has the capacity to deplete the diversity of native ants on the trees and within other strata of the ecosystem.

The evidence presented in this chapter also indicates that dominants within the mosaic have a considerable impact on the composition of the other invertebrates which occur on the trees. There are a number of reasons for this including the following:

1. *The existence of species-specific ant–Homoptera associations.* That cocoa is attacked by a wide variety of Coccoidea is well documented for Ghana (Strickland, 1951a, b), Brazil (Silva, 1944, 1950) and Papua New Guinea (Szent-Ivany, 1961). Many of these homopterans are tended by ants from a single species, from throughout a genus or by a subset of ant genera occurring within the crop (see review in Entwistle, 1972: 131–3). Since ant-tended homopterans may experience enhanced survival as a result of better waste removal, provision of ant-built shelters, the carrying of animals to new feeding sites and the predation of the homopterans' natural enemies (Hölldobler and Wilson, 1990), each block of the mosaic will tend to have its own distinctive homopteran fauna.

2. *The preference of particular dominants for particular prey types or prey size ranges.* This is evident from the association analyses between dominant ants and

(a)



(b)

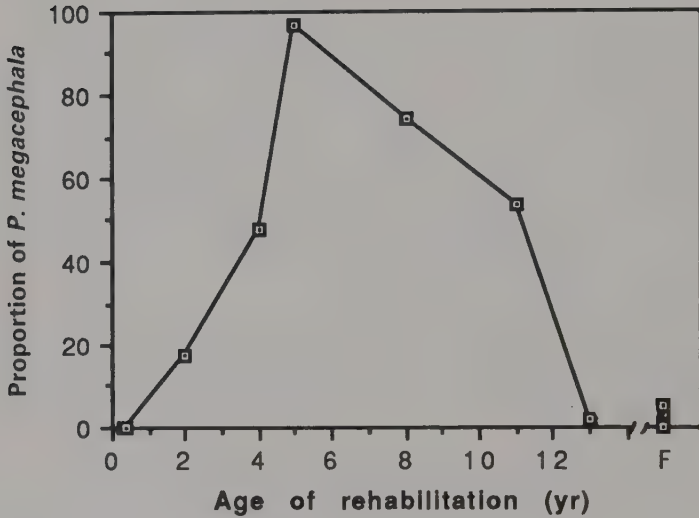


Fig. 5.9. Relationship between (a) ant species richness and (b) proportion of *Pheidole megacephala* caught in pitfall traps with age of rehabilitation in mineral sand mines at Richards Bay, Kwazulu, South Africa. The three points corresponding to 'F' on the horizontal axis are for undisturbed coastal dune forest (adapted from Majer and de Kock, 1992).

cocoa fauna in Ghana (Majer, 1976c) and Papua New Guinea (Room and Smith, 1975), which clearly show that certain insects are negatively associated with certain dominant ants. Some of these relationships exist because the ants and associated animals are responding to the same environmental factor; others represent direct biological relationships such as predation or harassment of the animal. There is evidence from the Brazilian data presented earlier in this chapter that some ants may prefer prey within a particular size range. Whether the ant is selecting on the basis of prey type or prey size range, the dominant ant has the capability to influence the make-up of the invertebrate community occurring within its territory.

3. *The possession of generalist or specific feeding regimes by the dominant ant.* Mention has already been made of the relationship between diversity of the non-dominant ants and the degree of specialization of the dominant ant. The evidence from Ghana and New Guinea suggests that the least specialized ants, *C. striatula* and *T. albipes* respectively, supported the highest level of cocoa pests (Majer, 1976c; Room, 1975a) and for the former species at least, the highest diversity of invertebrates (Majer, 1976c) associated with them.

4. *The multiplier effect of different parasite and/or predator species occurring in areas where particular herbivores are present.* This is well illustrated in Papua New Guinea cocoa where the curculionid *P. szentivanyi* is negatively associated with the dominant ant *A. longipes*. The curculionid's parasites, *Nephrotoma* spp. (Tipulidae) are positively associated with the distribution of their host, and thus also exhibit a distribution pattern which is affected by the ant (Room and Smith, 1975).

5. *The physical and biotic nature of the environment within the territory of each dominant.* This can result from the tendency for particular dominants to occur within particular shade or other environmental regimes; examples of different dominants preferring differing cocoa shade regimes in Ghana are given in Majer (1976b), while Room and Smith (1975) have provided examples from New Guinea cocoa in which certain invertebrates exhibit distributions which are influenced by the same shade regimes which influence the dominant ant. In addition, the changes in vegetation which can result from the degree of herbivory which different dominants allow within their territory (Gilbert, 1980) also have an impact on the other invertebrates. In Papua New Guinea, for example, *A. longipes* is linked to good cocoa canopy due to its excluding the serious curculionid pest *P. szentivanyi* (Room and Smith, 1975). The luxuriant cocoa environment then provides conditions suited to a whole range of other invertebrate species. The fact that dominant ants are acting as keystone species (Risch and Carroll, 1982), which have a major impact on the composition of the canopy fauna rather than merely coinciding with different invertebrate sub-communities along environmental gradients, is confirmed by Majer's (1976c) ant manipulation experiment; changes in the dominant species lead to changes in the associated invertebrates.

To summarize, the non-dominant ants and the invertebrate community in general tend to have a structure and diversity which reflect the composition of the ant mosaic. There has been considerable debate about the role of species-specific food webs leading to high invertebrate diversity in the tropics (Erwin, 1982); although the predicted value of 30 million insect species is perhaps somewhat of an overestimate (Basset, 1990; Stork and Gaston, 1990). On the basis of what has been described in this chapter, it appears that the impact of the ant mosaic is superimposed upon what Gilbert (1980) refers to as the 'chemical mosaic' of different plant species, and both act in tandem to enhance the diversity of the invertebrate fauna. The canopy of a large rain forest tree could well support two or more 'blocks' of dominant ants. In such a case the diversity of the canopy fauna could be greater than that which might be expected if the tree supported no, or one, dominant ant. This could be a contributory factor to the high diversity of ants which Wilson (1987) observed on one species of tree in Peruvian rain forest. To conclude, the ant mosaic is an important contributory factor to invertebrate diversity in the tropics.

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Bees, Pollination Systems and Plant Diversity

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Pollination is an exceedingly important aspect of angiosperm life history. It has frequently been argued that the diversification of pollination systems has been one of the most important factors in the radiation and success of flowering plants (Regal, 1977; Crepet, 1984; Willemstein, 1987). Substantiation for the importance of changes in pollination biology as causes of plant diversification is seen by many to be reflected in the spectrum of pollination schemes found in modern plant communities. Implicit in an hypothesis that links pollinator diversity with evolutionary diversification of floral hosts is that there is a high level of specificity between plant species and their pollinators, and therefore opportunity for rapid generation of reproductive isolation mechanisms. Specificity could be fostered by floral morphologies, reward systems, or phenologies that become specialized to facilitate visitation by one class of flower visitors and to exclude others. Such specializations appear to be reflected in the classic floral syndromes of 'moth' flowers, 'butterfly' flowers, 'hummingbird' flowers and the like (Faegri and Pijl, 1979). These arguments have been used to stress the importance of diversity in pollination systems as causes of plant diversity but the same kinds of reasoning about specificity lend support to the hypotheses about the maintenance of flowering plant diversity within communities.

The importance of diversity of pollinators in maintaining plant diversity is easily seen in cases in which the absence of a particular pollinator group will almost certainly lead to reproductive failure, and ultimate community exclusion, of plants dependent on that group for pollination services. The importance of diversity *within* major pollinator groups is less clear because plant pollinator interactions commonly involve fairly broad levels of adaptation rather than close species-to-species mutualisms. For example, for plants dependent on humming-

birds for pollination, it makes a substantial difference if the hummingbirds involved are short billed, commonly territorial species, or long-billed, trap-lining taxa. However, once beyond these ecological distinctions, it apparently makes little difference to plants if there are two or 20 species of hummingbirds in a community since birds of a particular ecological guild tend to be functionally equivalent (Feinsinger, 1983). Insects, however, often show much higher levels of specificity to hosts than vertebrates. Within insects, bees are commonly thought to be the most abundant group of flower visitors and, because of their extremely high dependence on floral resources throughout their life histories, good candidates for close links between pollinator diversity and floral diversity.

With an estimated 20000 (Hurd, 1979) to 30000 (Gauld and Bolton, 1988) species, the bees are arguably both the most diverse and familiar group of aculeate Hymenoptera. While their familiarity is largely due to the ubiquity of the domesticated honeybee, the ecological significance of bees lies in their role as pollinators in natural plant communities. Plant reproductive success may frequently be limited by pollinator activity (Bierzychudek, 1981) so it has been proposed that competition for pollinators may play an important role in structuring plant communities (Heithaus, 1974; Heinrich, 1975; Pleasants, 1982). Many mechanisms have been proposed which might function to minimize competition for pollinators. Examples include utilization of different pollinator species or guilds, flowering at different times, and differences in floral morphology or reward systems that might foster constancy of individual pollinators (Pleasants, 1983). Bees, particularly honeybees, are frequently claimed to be the single most important group of pollinators (Müller, 1883: 46; Free, 1970: 2; Proctor and Yeo, 1972: 146; Barth, 1985: 28) although more radical claims that honeybees are responsible for as much as 80% of all insect mediated pollination (Barclay and Moffett, 1984) appear to be pure speculation (Torchio, 1990).

There is a variety of reasons why bees are commonly assumed to be such important pollinators. The most obvious is simply that bees are highly 'motivated' flower visitors. With the exceptions of minor patterns such as collection of honeydew (Crane and Walker, 1984), fungal spores (Shaw, 1990), or carrion (Roubik, 1982), the economies of bees are based almost entirely upon floral resources. Unlike most other flower visiting groups for which floral resources provide only energy for adult flight, or perhaps protein for egg maturation, bees are completely dependent on floral resources during both the adult and larval stages. The high degree of dependence on floral resources is reflected in the numerous adaptations of bees for a floral diet, a range of adaptations far exceeding that seen in other flower-feeding groups (Müller, 1883; Thorp, 1979). This high dependency requires floral visitation rates by bees above what might be expected simply on the basis of adult biomass or metabolic requirements. Females of some solitary bee species harvest four or more times their own body weight in pollen and nectar each day while provisioning multiple nest cells (Danforth, 1990; JLN, pers. obs.). The number of flowers visited during a single foraging trip may vary from one to thousands, depending on the requirements of

the bee and levels of resource availability. One estimate suggests that under typical field conditions, production of a single gram of honey from red clover by workers of *Bombus fervidus* requires 90 hours of bee labour and visitation to 211 200 florets (Heinrich, 1979: 145). The close interactions of bees and flowers have facilitated the evolution of numerous secondary systems involving mimicry and ancillary resource systems (Simpson and Neff, 1981, 1983). In addition, the relatively sturdy construction of bees, at least partially a legacy of their derivation from predacious ancestors (Malyshev, 1968; Lomholdt, 1982), allows for structural bee-flower interactions not possible with more physically delicate flower groups such as Diptera or Lepidoptera. Similarly, the advanced flight and navigational abilities of bees, another legacy of their central place foraging predacious ancestors, enhances the ability of bees to exploit widely scattered flowers. Although data remain limited, there is evidence that bee population sizes tend to be more stable than those of other insects (Wolda, 1983; Roubik, 1989), thus enhancing the relative ability of bees to exert selective pressures as pollinators.

In the following sections of this chapter we examine data on the importance of bees as pollinators in natural communities and attempt to unravel some of the links between bee diversity and plant diversity. We also examine some of the special features of bee diets and foraging behaviour (oligolecty and floral constancy) that contribute to the importance of bees as pollinators. Finally, we examine some of the factors associated with bee pollination that may be important in structuring plant communities.

Importance of Bees in Natural Communities: Some Examples

While interest in the roles of different insects as pollinators in different communities dates back at least into the nineteenth century (Müller, 1880; Robertson, 1895), the study of community-level plant/pollinator interactions remains largely in its infancy. When comparing importance values of pollinators on a community level, it is not always clear what constitutes a dominant pollinator group since any number of criteria could be used: abundance, species diversity, or efficacy at removing or depositing pollen. In addition, in virtually all studies at the community level, 'who pollinates what' is usually determined by a series of educated guesses. Guesses about successful pollinators are likely to be quite accurate in cases of highly restrictive floral morphologies, specialized resource types, or cases where only one visitor type is ever observed on a particular floral host. Suppositions become increasingly problematic as the range of visitors to any particular flower increases. Much progress has been made in understanding the species composition, relative abundances and phenologies of the flower visiting faunas of a number of communities, but these are only first steps in understanding the importance of various groups as pollinators. Experimental studies have shown that different visitors to a particular flower may vary widely in their relative efficacies as pollinators (Primack and Silander, 1975; Spears,

1983; Schemske and Horvitz, 1984). Even when disparate visitors converge in terms of pollen deposited per visit, they may vary greatly in their impact on plant fitness if they move pollen differently between flowers. Differential efficacies as pollinators can arise because of variation in absolute distance of inter-flower movement (Schmitt, 1980), or through variations in carryover of pollen between visits (Thompson and Plowright, 1980; Waser and Price, 1983). It has also been argued that the relative importance of various pollinators may depend on the ability to deliver particular mixes of genotypes (Janzen, 1977). This last factor may be particularly important in situations in which seed set is relatively insensitive to the amount of pollen deposited. The quality of pollens deposited is important if seed set is related to pollen tube competition that may affect mating success (Snow and Spira, 1991) or enhance fitness or progeny (Mulcahy, 1979). Finally, although there is much speculation, virtually nothing is known of the actual energetic efficiencies of different pollination systems (the costs of moving pollen x metres or receiving y pollen grains) in real communities.

While no studies fully examine the importance of different pollinators in a complex community, the studies summarized below are useful first approximations of the relative importance of bees as pollinators in different communities. Our sample of communities is heavily slanted towards studies in the Americas. This bias reflects a real emphasis in the literature as well as an attempt to include systems with which we have some personal familiarity.

Temperate zone

Deserts and desert scrub communities

Bees are clearly the dominant pollinators in the few deserts and desert scrub communities that have been studied to date. Bees are the primary or co-dominant pollinators of all 15 of the dominant woody perennial species in a Monte Desert site in Argentina (Simpson, 1977; Neff *et al.*, 1977; Neff, unpublished). The pre-eminence of bees as pollinators was also clear, but less so, at a study site in the northern Sonoran Desert of Arizona. At this site, at least eight of the 15 dominant perennials were primarily bee pollinated (Simpson, 1977). Bees were also the most important pollinator group for most of the cacti (not included in Simpson's survey), herbs, and vines at both sites (Neff, unpublished).

Using a somewhat different methodology, Moldenke (1976, 1979b) found bees were the most important pollinators in two arid sites in Chile and in a third in California. However, a rather high proportion of the flora at all sites was autogamous and/or rarely visited.

Mediterranean scrub communities

Moldenke (1976, 1979b) has studied a series of Mediterranean scrub communities (warm temperate shrublands with winter rain, summer drought

regimes) in California and Chile. The pollination spectra of these areas appeared to be more diverse than that observed in warm deserts, but bee pollination, primarily by solitary taxa was the most prevalent system. An estimated 40% of the flora in both areas was calculated to be primarily bee pollinated. Large numbers of small oligolectic bees were associated with many of the dominant taxa in the California chaparral but the efficacies of these bees as pollinators remain unclear.

Forests

Temperate forests characteristically have a high proportion of their biomass (the dominant trees), but not their diversity, pollinated by wind. An analysis of 22 communities of the eastern and western slopes of the Cascade Mountains indicated that flies, followed by bees were the dominant pollinators (Del Moral and Standley, 1979). However, the determination of principal pollinators was based on floral morphology and literature reports in this study rather than on direct observations. Such methods may yield inaccurate estimates of who pollinates what, particularly when dealing with seemingly unspecialized flowers (O'Brien, 1980; Lindsey, 1984).

The importance of various potential pollinators in temperate forests may vary with the degrees of shading of the forest floor. Commenting generally on California pollination systems, Moldenke (1976) indicated that bumblebees were the most important pollinators in closed, heavily shaded environments although all types of pollinators were scarce. Solitary bees became increasingly diverse and abundant in more open forests, becoming the most important pollinating group in some habitats. However, oligolectic species apparently played a minimal role in these areas (Moldenke, 1976).

Pollination systems in North American Eastern Deciduous Forest vernal annual communities where most flowering occurs during the relatively brief period before canopy closure, have been studied in considerable detail. All eight species studied at a site in Illinois were primarily bee pollinated (Schemske *et al.*, 1978). Pollen limitation of fruit set was observed in one of the two bumblebee pollinated species, apparently due to the scarcity of visits. The other flowers were visited by a mix of solitary bees, primarily *Andrena* spp. and syrphid flies. Oligolectic bees seemed to play no major role as pollinators although it was suggested that the observed pollen limitation of fruit set in *Erythronium albidum* (Liliaceae) was due to the rarity of the specialist, *Andrena erythronii*.

In a study of 12 vernal forest herbs of a North Carolina community, Motten (1986) found bees were the most important pollinators. However, a bee fly, *Bombylius major* (a parasite of solitary bee nests), was a major pollinator of several species. Most plants had relatively unspecialized pollination systems, and were visited by a variety of generalist taxa. In the one system where an oligolectic bee was one of the most abundant visitors, it was found to be no more effective as a pollinator than a generalist bee fly, at least on a fruit set per visit basis. Pollen

limitation of fruit set was observed only in the three species dependent on bumblebee queens as pollinators.

Montane communities

Several studies have reported decreases in the abundance and diversity of Hymenoptera (including bees) with increasing altitude. This pattern suggests a decrease in the importance of bees as pollinators at high elevations where Diptera or Lepidoptera becomes correspondingly more important (Müller, 1880; Warren *et al.*, 1988). Because of their high requirements for floral resources, bees may be at an ecological disadvantage in harsh, cold, high altitude environments (Arroyo *et al.*, 1982, 1985). Nevertheless, examination of a series of community pollination studies paints a mixed picture of the role of bees as pollinators in such habitats.

Bees were the primary pollinators of 50% of the zoophilous flora in an altitudinal series of communities in the Andes of central Chile, but there was considerable variation with altitude (Arroyo *et al.*, 1982). Bees were the primary pollinators of 67% of the zoophilous flora at the lowest site (2200–2600 m) but this percentage dropped to 13% at the highest elevation (3200–3600 m) where fly pollination predominated. Bumblebees were present at the highest elevations, but appeared to play a relatively minor role as pollinators.

A study of five communities at 2900 to 4100 m elevation in the Rocky Mountains of Colorado indicated bees were the most important pollinators at all sites even though flies were more diverse than bees at the highest elevations (Moldenke and Lincoln, 1979). Bumblebees were the most important single group of pollinators, pollinating 29% of flora. Most plants were visited by a range of visitors although *Aconitum* and *Delphinium* (Ranunculaceae) were pollinated almost exclusively by long-tongued *Bombus* spp. Species in two additional genera (*Erythronium* and *Campanula*, Campanulaceae) appeared to be dependent on oligolectic bees. Moldenke (1976) obtained similar results from studies of four alpine and subalpine communities in the Sierra Nevada of California. In all four communities, generalist bees, primarily bumblebees, were the most important pollinators. Specialist taxa constituted the largest proportion of the bee faunas, but their population sizes tended to be quite small and their role in pollination apparently limited.

All the montane communities mentioned above have relatively complex bee faunas, in terms of species number, morphological diversity and life histories. In contrast, Inouye and Pyke (1988) found that the bee faunas of montane and alpine communities in the Snowy Mountains of Australia consisted almost entirely of solitary, short-tongued bees (mouthparts < 3.0 mm). The authors did not attempt to classify flowers in pollination types, but pollination systems appeared to be quite generalized with flies as the predominant pollinator group. Fly visits represented 62% of total recorded floral visits and flies were the major visitors to 56% of the flowers studied. Bee visits made up only 31% of total

flower visits and bees were the major visitors to only 30% of the flora. Inouye and Pyke (1988) suggested that the low floral diversity in the Australian montane communities reflected the absence of long-tongued bees (bumblebees).

Tropical habitats

Lowland evergreen forests

No complete inventory of pollination systems is available for any tropical rain forest community, presumably reflecting the great structural and floristic complexity of these habitats. Putative pollination systems for 143 of the roughly 400 tree species at the La Selva Biological Station, Costa Rica have been analysed by Bawa and co-workers (Bawa *et al.*, 1985). They judged bees to be the primary pollinators or co-pollinators of 40% of the tree species, making them the most important single group of pollinating agents. Although they made no fine taxonomic distinctions between bee taxa, Bawa and co-workers emphasized the division of pollination systems into two classes: one involving medium to large bees (euglossines and anthophorids), and one involving small bees (halictids, megachilids and meliponines). Large to medium bee systems involved 27.5% of the tree species and were evenly divided between canopy and subcanopy taxa. Small bees appeared to pollinate 14% of the tree species, most of which occurred in the subcanopy. An additional 15.8% of the tree species was considered to be pollinated by small, diverse insects, a category that included, but was not restricted to, small bees. A study combining data from savannah and lowland communities in French Guiana also indicated a basic division into plants visited by large, and those visited by small, bees (Roubik, 1979, 1989: 319).

Deciduous dry forests

Large bee pollination systems (defined by the authors as bees honeybee-sized or larger) of a Costa Rican dry forest have been studied in considerable detail by Frankie *et al.* (1983). They considered the 45 species of the large-bee guild to be the primary pollinators of 25.5% (74 of 290) of the trees and climbers in this community. However, these bees were the primary pollinators of only 11 species of herbs, shrubs and epiphytes. They judged small bees to be the major pollinators of an additional 75 species of plants. Within the large bee guild, a major division was noted between the anthophorines (mainly *Centris* spp.) and euglossines. The former were active largely in the dry season when they foraged on various mass-blooming species; the latter tended to have an activity peak in the wet season but foraged throughout the year on widely scattered, long blooming taxa. Although all the 'large' bees visited a wide array of pollen and nectar hosts, an experimental manipulation of plant heights indicated some height selectivity, suggesting differential preferences for foraging among some bees in the canopy rather than the understorey (Frankie and Colville, 1979). Although not speci-

fically discussed by Frankie and co-workers, the seven species of Malpighiaceae in the dry forest are presumably dependent on oil or pollen collecting female centridine bees as pollinators (Vogel, 1974; Raw, 1979).

Other communities

Bees are reported to be the dominant pollinators in a number of other neotropical communities. Percival (1974) found solitary bees, butterflies and hummingbirds to be the most important pollinators during the dry season in a coastal scrub community in Jamaica, although no precise delineation of who pollinated what was given. European honeybees were present and apparently capable of pollinating 18 of the 21 taxa they visited. Similarly, Ramírez (1989) reported that bees were the major pollinators of 51% (28 of 55) of the plant taxa he studied in a shrub community in the Alta Guyana region of Venezuela even though relatively few bee species (24 species in four families) were observed. He indicated that medium-sized bees were more important as pollinators than either large or small bees in that system. Zapata and Arroyo (1978) showed that bees were the major, or exclusive, pollinators of 17 of the 22 plant species they studied in the secondary deciduous forest in Venezuela. However, neither Ramírez nor Zapata and Arroyo made any fine distinctions about the roles of particular bee taxa.

Further south in Brazil, Gottsberger *et al.* (1988) studied the pollination biology of ten species of a simple tropical beach dune community in São Luis, Brazil. They found nine of the ten species to be bee pollinated. *Centris lepreiuri*, the only bee nesting on the beach, visited the largest number of species (six) of any of the bees he observed. Several flowers appeared to be specialized for pollination by large bees.

Summary of community studies: climatic and biogeographical correlations

In most of these surveys, a pollinator class estimated to visit the largest number of plant species in the community studied was considered to be the 'most important' group of pollinators. The combined data from these community surveys yield ample, albeit indirect, evidence that bees are the most important group of pollinators in a wide range of habitats. However, this finding sheds little light on how bees as pollinators may foster plant diversity within particular communities or how bee diversity may be related to plant diversity.

On a broad geographic scale, bee species richness is believed to be greatest in temperate warm xeric or warm mesic habitats rather than the floristically more complex moist tropics (Michener, 1979). Three hundred or more bee species have been reported from many limited areas in the temperate zone, a number exceeding that found at any equivalent site in the tropics (Michener, 1979). The total of 439 bee species known to occur within 16 km of Riverside, California (Timberlake, cited in Michener 1979) is greater than the bee fauna of all of

Panama (Michener, 1954), one of the best studied tropical regions. If bee diversity really is highest in the temperate zone, clearly no simple link between bee diversity and plant diversity is likely, given the high floristic diversity found in many tropical habitats (Gentry, 1983). However, some caution is necessary when making temperate-tropical comparisons of bees. The study areas on which the various faunal lists are based vary widely in size, often include a variety of plant communities and may reflect widely varying years in terms of data collection. As a result, it is rarely clear exactly what is being compared. Moreover, comparatively few bee faunal studies have been undertaken in the tropics.

Short-term studies, which presumably present a more accurate picture of the real number of interacting species in a given community, paint a more ambiguous picture. The number of bee species (183) found during a one year study of a tropical deciduous forest in Costa Rica (Heithaus, 1979) exceeds the number of bee species (23 to 176) found in any of the California communities studied by Moldenke (1976, 1979a,b,c) and approaches that (188 species) recorded in the richest desert communities (Neff *et al.*, 1977). However, it should be noted that the 183 species discussed by Heithaus (1979) represent the combined faunas of two habitats, a complex deciduous forest with 170 bee species and a simple deciduous oak forest with 87. This 'community' may therefore not be strictly comparable to the temperate community figures. Defining what constitutes a community is often a problem when comparing ecological studies. None the less, if lowland neotropical rain forest habitats really contain the 200 to 300 bee species claimed by Janzen (1975), bee species number in tropical habitats may frequently exceed that found in single habitats in the temperate zone. Regional differences, if real, might reflect differences in beta diversity rather than real differences in a number of co-occurring species. At the moment, biogeographic diversity patterns do not appear to be particularly supportive of a close causal role for bee diversity as a factor promoting plant diversity. However, current data do not exclude the possibility of such a relationship.

A more appropriate comparison might be to look at the relationship between bee diversity and plant diversity in particular habitats. Positive correlations of bee diversity and plant diversity cannot prove bee diversity fosters floral diversity since plant diversity might drive bee diversity. It is also possible that the two are independent of one another but correlated with a third factor such as environmental productivity or stability. None the less, finding a positive correlation would be a minimal criterion for establishing the role of bee diversity in fostering plant diversity. Unfortunately, comparisons of different studies are difficult due to differing methodologies and methods of presenting data. Positive correlations between bee diversity and the number of putatively bee pollinated (or at least visited) plants are evident in the studies in Costa Rica (Heithaus, 1974, 1979) and Chile (Arroyo *et al.*, 1982). In the Chilean study, the number of bee pollinated plants in different communities declined with number of bee species, while the number of plants pollinated by other insects (Diptera and Lepidoptera) stayed constant. In the Costa Rican study, bee diversity and the number of bee visited

plants and the number of plants visited by animals other than bees all declined together. Our analysis of the data from 22 plant communities in California and Chile studied by Moldenke (1975, 1976, 1979b) failed to find a significant correlation between the number of bee species and either total number, or the number of putatively bee pollinated, plant species. However, this analysis is problematic since Moldenke used multiple, non-exclusive categories for bee pollination making it difficult to ascertain what proportion of the flora in a particular community is bee pollinated.

The preceding observations from biogeography and community studies appear to provide little in the way of evidence to support a direct link between bee diversity and plant diversity. This lack of a relationship may simply reflect the fact that plant-pollinator interactions frequently appear to be quite diffuse, with plants interacting with a variety of potential pollinators rather than a single pollinator (Baker and Hurd, 1968; Moldenke, 1976; Schemske, 1983; Feinsinger, 1983). If there is no direct relationship between diversities it might be concluded that the thousands of bee species found in different ecosystems are of limited ecological significance. We argue below that while many bee species may indeed be marginal to overall ecosystem function, a critical level of bee diversity is important and vital in the maintenance of plant diversity in many communities.

Features of Bee Biology and the Maintenance of Plant Diversity

It is easy to envision theoretical communities in which a restricted array of pollinators services a diverse array of plants. All that would be needed is a long-lived, behaviourally labile pollinator species composed of individuals capable of at least short-term constancy to a particular floral type. Many bees, particularly social species, forage in exactly this way. Individual bees in the colony tend to be short lived, but the colony as a whole has a long life expectancy. Within a community, the only prerequisites for ensuring constancy to plant species are enough differences in floral attraction systems and/or phenology to permit constancy of individual bees. For such a system to operate, similar flowers would be expected to differ in their blooming or reward presentation schedules. Conversely, flowers with similar reward structures and phenology would be expected to differ in morphology. While some communities, such as the bogs studied by Heinrich (1976a) and the meadow studied by Pleasants (1982) seem to function in such a manner, this simplistic pattern appears to be atypical.

As has been documented in many compendia, angiosperm pollination schemes have radiated widely and involve many different animal taxa (Müller, 1883; Faegri and Pijl, 1979). Even within the primarily melittophilous portions of a flora, pollination schemes are so diverse that only in the simplest of communities is it likely that a single bee species or small group of taxa would provide adequate pollinator services. Co-existing plants generally exhibit a wide range of floral sizes, shapes and reward structures. These features represent parameters

that are often correlated with bee diversity. Below we address some of the ways in which bee diversity is linked to plant diversity in natural communities and show why it would be impossible to maintain current levels of plant diversity in most communities if bee diversity were drastically reduced.

Flower size and structure

While a variety of bee species with widely varying body sizes may be involved in the pollination of plants with open systems, e.g. *Prosopis* (Simpson *et al.*, 1977), many pollination systems require a proper match of bee and flower size. All successful systems require the pollinator to contact the pollen presenting structures (for pollen donation) and the stigma (for pollen receipt). If a bee is too small for a particular flower, it may frequently miss the anthers, stigma, or both, so that pollination rarely, if ever, occurs. If a bee is too large for a flower, it may avoid the flower altogether, or fail to work the floral mechanism properly. Since bees range from under 2 mm to over 32 mm in body length, a linear range that represents more than 3000-fold difference in body mass, there is ample opportunity for specializations of flowers for different size classes of pollinating bees. Examples of flowers dependent on large bees include species of *Aconitum* (Ranunculaceae), *Centrosema* (Fabaceae) and many members of the Bignoniaceae and Lethycidaceae. Because of their relationships with large bees, these flowers are showy to us and consequently easily recognized. Flowers specialized for very small bees may be inconspicuous and thus less familiar.

Large bees may often play roles as pollinators disproportionate to their abundance, particularly for widely dispersed plants. Unfortunately, little is known of the foraging ranges of most bees and even less of real pollen flow distances as a result of their activities. Honeybees occasionally forage at distances of 11 km or more from the hive (Frisch, 1967) and the median foraging distance may be roughly 2 km under natural conditions (Visscher and Seeley, 1982). However, such distances may greatly overestimate actual pollen dispersal since most long flights are between the hive and discrete resource patches, not between widely scattered conspecific plants. Honeybee-mediated pollen dispersal between widely scattered plants may occur if there is extensive pollen transfer between workers in the hive (DeGrandi-Hoffmann *et al.*, 1986) although the extent of such transfers remains controversial (Buchmann *et al.*, 1990). On the other hand, some large solitary bees are believed to move regularly between widely scattered flowers or inflorescences, perhaps employing so-called 'trap lining' behaviour (Janzen, 1971). Restricted trap lining has been documented for some *Bombus* spp. (Heinrich, 1976b; Thompson *et al.*, 1982) but no large-scale trap lines involving widely scattered plants have actually been mapped. Still, a variety of large bees (various euglossines, bombines, xylocopines and diphaglossines) are likely to be important pollinators of widely scattered flowers since they have demonstrated the high precision place memory and navigation abilities necessary for such activities (Janzen, 1971; Ackerman *et al.*, 1982). While it is not at all

clear that the extreme distance of 23 km recorded for *Eulaema surinamensis* (Janzen, 1971) represents the usual foraging range of large bees, mark release studies suggest some *Xylocopa* species may have foraging ranges of 5 km or more (Balduf, 1962; Kapil and Dhaliwal, 1969 cited in Roubik, 1989). Anecdotal evidence suggests long distance foraging may be common in *Bombus* as well (Heinrich, 1979; Roubik, 1989).

Resource systems

Pollen

OLIGOLECTY

Because of its chemical and physical complexity, pollen provides numerous opportunities for specializations of bees to a particular pollen type. The term oligolecty was coined, in fact, for the restriction of pollen collection by female bees to a particular species or limited set of plant taxa. Oligolectic bees frequently display morphological and behavioural adaptations which facilitate collection of pollen from their preferred hosts (Linsley, 1958; Thorp, 1979). Nevertheless, the mechanisms underlying oligolecty remain poorly understood. Some authors suggest it may reflect little more than larval conditioning with females collecting the same pollens on which they originally were reared (Linsley, 1978; Feinsinger, 1983). Larval conditioning may play a role in oligolecty, but we are aware of no hard evidence to that effect, and fail to see how it could maintain the observed hierarchies of host choice through space and time. Other factors likely to contribute to the maintenance of oligolecty include enhanced foraging efficiency (Strickler, 1979; Lavery and Plowright, 1988), use of pollen hosts as mating sites and differential efficiency in larval utilizations of pollen of different plants. The last of these factors is the most poorly understood. Differences in larval growth rate and survivorship have been demonstrated for two polylectic bees raised on pollens of various plant taxa, suggesting pollen chemistry could be an important factor in bee host choice (Levin and Haydak, 1957; Guirguis and Brindley, 1974). However, at least one oligolectic species has been successfully reared on pollen unrelated to its usual host (Bohart and Youssef, 1976). In situations with a wide variation in resource quality, using a restricted set of cues to recognize 'good' hosts amidst a sea of 'bad' hosts results in some acceptable pollen hosts (from the larva viewpoint) being ignored as food.

Oligolectic bees are distributed unevenly both geographically and taxonomically over the range of potential floral hosts. Oligolectic bees may comprise as much as 66% of the temperate warm desert bee fauna, but typically less than 25% of the bee faunas of most forested regions of North America (Moldenke, 1979c). While oligolectic bees are associated with more than 40 plant families of the North American flora, more than one-third of all specialists are associated with the Asteraceae (Moldenke, 1979c). Other families with large numbers of associated oligolectic bees include the Fabaceae, Malvaceae, Onagraceae and Cactaceae.

The interactions of oligolectic bees and their host plants are sometimes referred to as co-evolved (Moldenke, 1979c), but the term is improperly applied in most such interactions (Feinsinger, 1983; Schemske, 1983). There are no strict one-to-one examples of a particular plant species being dependent on a single oligolectic bee species throughout its range. Most plants used by oligolectic bees can potentially be pollinated by a wide range of visitors. The evolutionary interactions of oligolectic bees and their floral hosts generally appear to be asymmetric. Oligolectic bees frequently show signs of adaptation to their floral hosts, but there is little evidence for reciprocal adaptation of flowers to their oligolectic visitors. This asymmetry is not surprising since oligolecty represents a form of host specialization by a herbivore, not specialization for pollination. Bees do not visit flowers to pollinate them; they visit them to fulfil their own requirements. Unlike fig wasps or yucca moths, there are no immediate benefits accruing to a bee if it becomes a better pollinator. It is thus not surprising that some oligolectic bees are no more than scavengers, having no direct role in the pollination of their floral hosts (Linsley *et al.*, 1963a,b; Michener, 1979). In other cases, oligolectic bees have proved to be no more effective pollinators of their preferred hosts, at least on a per visit basis, than other, more generalized, visitors (Tepedino, 1981; Motten *et al.*, 1981; Cane *et al.*, 1985; Neff and Simpson, 1990). However, our own observations in arid and semi-arid habitats (Simpson and Neff, 1987, and pers. obs.) as well as those of others (Linsley *et al.*, 1963a,b; Hurd and Linsley, 1975; Hurd *et al.*, 1980) indicate that in many localities, oligolectic bees frequently are the most effective pollinators of their host plants. From the plant viewpoint, an obvious advantage of an oligolectic pollinator is that it displays high constancy independent of the abundance of other flowers in the community. The importance of oligolectic bees as pollinators might be expected to vary with the extent of competition for pollinators.

While no generalizations can be made, it appears likely that some plant species in most temperate communities are dependent on oligolectic bees for successful pollination. Consequently, local extinctions of these bees could result in some level of reduction in plant species diversity.

VIBRATILE POLLINATION SYSTEMS

The term vibratile pollination is used for a wide array of pollen-collecting systems involving anther vibration by bees. The system is highly restrictive only in cases of nectarless flowers which present pollen in poricidal (or some functional equivalent) anthers as the only floral reward. Such systems are found in at least 54 families and 357 genera of angiosperms (Buchmann, 1983). Familiar examples include members of such genera as *Cassia* s. lato (Fabaceae), *Dodecatheon* (Primulaceae), or *Solanum* and *Lycopersicon* (both Solanaceae). Only the restricted set of bees (and a few flies) capable of properly vibrating or 'buzzing' the anthers to extract the hidden pollen are regular visitors, and therefore pollinators, of such flowers. The ability to employ vibratile pollen collection is widespread, but not universal among bees. It is common among colletids, halictids,

anthophorines and xylocopines, but is rare among andrenids and megachilids. Although most apids are capable of vibratile pollen collection, the common honeybee apparently is not (Buchmann, 1983). Since bees capable of vibratile pollen collection are quite widespread, it is not clear to what extent local extinctions of such bees would limit plant reproduction. It is, however, another example of bee taxa, even broadly generalist taxa, that may not be interchangeable.

Nectar

Nectar, the primary reward in most pollination systems, consists of an aqueous mix of simple sugars (typically glucose, fructose and/or sucrose) and small amounts of various secondary compounds (Baker and Baker, 1975). A number of surveys have found correlations between nectar composition and pollination by different functional groups of bees. Flowers presumed to be pollinated by bees with long mouthparts (>6 mm) tend to have higher proportions of sucrose (of total sugars) and higher amino acid concentrations in their nectars than flowers presumed to be primarily pollinated by short tongued (mouthparts <6 mm) bees (Baker and Baker, 1975; Baker and Baker, 1983). Although the correlations are suggestive, there is little hard evidence that nectar chemistry plays a decisive role in determining which bees visit a particular flower species. In theory, secondary compounds in nectar could limit (or promote) the attractiveness of particular flowers, to specific groups of bees (Bergdahl and Rhoades, 1981) in the same ways in which they appear to act in pollen. Such a process may operate in *Allium* (Liliaceae) where high nectar cation concentrations deter honeybee visits (Waller *et al.*, 1972). The fact that nectar chemistry does not play a more pronounced role in fostering specificity of pollinators, beyond energetic considerations, may be related to the physiology of its production and its use as an easily metabolized energy source.

Factors such as nectar volume and concentration, floral complexity and other features that limit access to nectar appear to be much more important than nectar chemistry in influencing flower choice by bees. All of these factors directly influence the caloric profitability of bee foraging. Since bees can never know *a priori* the actual distribution of floral rewards, they can never achieve 100% efficiency in foraging. Nevertheless they must make an energetic profit. Over the long term, costs of foraging cannot exceed energetic returns. Costs will vary with the requirements of individual taxa and environmental variables, but are expected to scale with size. Large bees require more energy per floral visit to gain a profit than small bees. Solitary flowers producing very small amounts of nectar cannot be profitable to, and are not visited by, large bees even though such flowers may be more than adequate for smaller bee taxa. The abundance of very small bees (body lengths 2–5 mm) and absence of larger bees at the tiny flowers of *Euphorbia* spp. (Euphorbiaceae) in the American south-west presumably reflects just such a situation.

At the other extreme, many flowers, particularly those rich in nectar, use a variety of structures to exclude small bees. Many species of Lethycidae can be pollinated only by large, strong bees capable of opening the complex flowers and gaining access to the hidden nectar and pollen (Prance, 1976). Numerous examples of plants dependent on bees with elongate mouthparts (as are seen in some Megachilidae, Anthophorinae, Bombinae and Euglossinae) can be found in families such as the Ranunculaceae, Fabaceae, Bignoniaceae, Scrophulariaceae and Lamiaceae. Systems rarely, if ever, involve one-to-one instances of co-evolution (Feinsinger, 1983) but the consequences of the loss of long-tongued pollinators (such as the loss of some long-tongued European *Bombus* spp.) are potentially catastrophic for plants dependent on them (Corbet *et al.*, 1991).

Fatty oils

Pollination systems involving the production of fatty oils as floral rewards provide some of the strongest examples of floral dependence by particular bee taxa. With their greatest diversity in the neotropics and temperate areas of South America, oil flowers are also found in the north temperate zone, southern Africa, and parts of the paleotropics. Some pollen transfer is possible via pollen collecting bees, but many oil-flower systems depend on oil-collecting bees. Within the oil-flower, oil-bee syndrome, there is a wide array of oil-collecting methods, resulting in the functional non-equivalence of some bee taxa (Neff and Simpson, 1981; Steiner and Whitehead, 1988; Vogel, 1988).

Some oil systems are fairly non-specific. It is likely that floral conservatism in the Malpighiaceae represents a general adaptation for functionally interchangeable oil-collecting bees as pollinators (Anderson, 1979). Nevertheless, there may be considerable geographic variation in the diversity of oil-collecting centridines visiting oil-producing malpighs. One study found as many as nine different oil-collecting centridines visiting, and apparently pollinating, flowers of *Byrsonima coccolobifolia* in the cerrado of Brazil (Gottsberger, 1986). On the other hand, some populations of Malpighiaceae in the Atacama Desert are dependent on a single species of *Centris* for pollination (Simpson, 1989). Many oil flowers of the Scrophulariaceae have complex floral morphologies and apparently are dependent on very restricted sets of potential pollinators, at least at any particular site (Vogel, 1974, 1988; Steiner and Whitehead, 1988; Simpson *et al.*, 1990).

Euglossine scent collection

Pollination systems dependent on the scent collecting activities of male euglossine bees provide other examples of highly taxon-dependent systems. For a wide array of neotropical orchids, and apparently some other taxa as well, male euglossine bees are the only floral visitors and pollinators (Pijl and Dodson, 1966). Although there is little doubt volatile oils are involved in euglossine mating systems, why male euglossines collect volatile oils remains unclear despite

much speculation, field work and experimentation. In an evolutionary sense, these pollination systems appear to be quite one-sided since the various orchids (and other plants involved in these systems) are far more dependent on the presence of euglossines than the bees are on these flowers (Feinsinger, 1983). Through a combination of floral complexity, specific mixes of volatile oils, and preferences of different euglossine bee species for particular volatile oils, many orchids that rely on male euglossines for pollination have very restricted sets of pollinators. A majority of these orchids are apparently dependent on a single species of euglossine bee for pollination (Roubik and Ackerman, 1987).

Resins

Flowers of a few plant taxa (primarily some members of *Dalechampia* (Euphorbiaceae) and *Clusia* (Clusiaceae)) are known to produce resins or similar sticky compounds as their primary rewards for pollinators (Armbruster, 1984). Such plants seem to be dependent on a restricted set of bees as pollinators. These bees, all female heriadinine or anthidiine megachilids, and meliponine or euglossine apids, collect resins for use in the construction of their nests. Indications of population level morphological adaptation of flowers for different size classes of resin bees as pollinators have been demonstrated for some resin producing taxa (Armbruster and Herzig, 1984).

Mimicry systems

Strict mimicry systems, in which a species produces no rewards and relies entirely on deceit, rarely constitute more than a very small proportion of the biomass in any particular community. Some mimicry systems, such as the pseudocopulatory systems in which flowers use a combination of morphological and chemical cues to deceive mate seeking males, may be highly specific. In the famous *Ophrys* system, a number of different species are dependent on the presence of very restricted sets of species of male bees as pollinators (Kullenberg and Bergstrom, 1976). Interactions in more general resource mimicry systems may not be so taxonomically narrow but may still be dependent on a fairly limited set of visitors (Thien and Marks, 1972; Little, 1983; Heinrich, 1979: 189–90).

Phenology

Many factors may be important in determining when particular plant species flower. These range from basic climatic factors to more complicated considerations of competition for pollinators or synchronization of flowering with the presence of particular pollinator groups. For bee pollinated plants, the two are easily confounded since it is frequently difficult to disentangle the causal relations of bee and plant phenology. Bees could be active during a particular season because their hosts flower at that time, or plant flowering could be constrained to

the times during which their pollinators are foraging. For most communities, it is therefore difficult to determine how particular bee life histories determine the reproductive success of their hosts. None the less, some generalities are possible.

At one extreme are the univoltine solitary species. These bees constitute the preponderance of species diversity, at least in most temperate communities. Such bees are highly seasonal and tend to have very short flight seasons (often only 3–4 weeks) which, for oligolectic species, may be synchronized with particular floral hosts. Communities dominated by solitary bees may have a high turnover through the year as shown by the fact that only 11% (21 of 188) of the bee species were active during both the spring and summer blooms in a Sonoran Desert community (Neff *et al.*, 1977). Most solitary bees overwinter as prepupae, a feature likely to be correlated with the ability of some species to spend two or more years in larval diapause (Torchio, 1975; Rust, 1988). In desert communities, such bees may behave like dormant seeds, waiting for the same environmental cues that trigger their floral hosts to germinate and/or flower to initiate their pupation and emergence. In theory at least, close synchrony of the flowing phenology of particular plants and their bee pollinators might allow an independence of a plant's phenology from the background of overall pollinator availability. In reality, there appear to be few clear examples of such decoupling involving bee-pollinated plants. Possible exceptions might include the flowering of some *Opuntia* spp. and other bee pollinated Cactaceae in the American southwest (Simpson and Neff, 1987).

A variant pattern involves various solitary bees which overwinter as adults (many *Andrena* and *Osmia* as well as some *Anthophora*, *Megachile*, and *Habropoda*) (Stephen *et al.*, 1969). Species in these groups are frequently the bees active earliest each spring in the northern hemisphere and are the important, sometimes the sole, pollinators of many early vernal angiosperms. Overwintering as an adult is presumably metabolically more costly than doing so as a prepupa but it facilitates early emergence by avoiding the problems associated with pupating during freezing or near freezing conditions.

A different type of interaction of bee and plant phenology is likely in situations involving primitively social species. In the temperate zone, bumblebees and many social halictines have annual colony cycles in which only new queens overwinter. Queens found new colonies each spring, foraging for a relatively brief period each spring in order to produce the first brood of (typically) much smaller workers. These workers then take over foraging duties and, resources permitting, the number of workers per colony increases through the season, culminating in the production of males and new queens that will begin the cycle anew. This pattern of colony growth produces a seasonal progression with relatively low densities of large pollen and nectar collecting queens early in the year, followed by increasing densities of smaller pollen and nectar foraging workers, and finally a mix of workers and large nectar foraging reproductives late in the year. These seasonal differences in the sizes and abundance of bees are likely to influence pollination systems through the season. Bumblebees play an important but quite

limited role in the pollination of spring flowering plants in the central Texas communities we have studied, as well as in some temperate deciduous forest communities discussed earlier. However, by late summer and autumn, bumblebees are the single most important pollinator group for a wide range of plant taxa (Neff and Simpson, pers. obs.)

Yet another type of phenological interaction between plants and bees is possible for long-lived solitary bees (some xylocopines and euglossines) and eusocial species with perennial colonies (apines and meliponines). The essentially continuous availability of such pollinators may be an important factor in permitting the existence of synchronous, aperiodic flowering in some bee pollinated tropical taxa (Augsburger, 1980; Appanah, 1981, cited in Roubik, 1989).

A final phenological interaction of bees and plants involves the daily restriction of flowering to matinal, crepuscular, or nocturnal periods. Most bees are active only during daylight hours but a number of taxa show various morphological and behavioural adaptations for foraging under conditions of extreme low light (Linsley, 1978). Interactions involving plants that flower at or before dawn, such as the *Cucurbita-Peponapis/Xenoglossa* system, provide some of the strongest examples of a high degree of dependence of a plant genus on a restricted set of oligolectic bees as pollinators (Moldenke, 1979c).

Conclusions

There can be little doubt that bees are an extremely important, or the most important, group of pollinators in a wide array of plant communities. Indeed, it is difficult to envision a world without bees. Other insects such as beetles, flies, wasps, moths and butterflies might be able to assume the role of bees in some cases but in many communities, large portions of the flora such as many caesalpinoid and papilionoid legumes are obligately dependent on bees as pollinators. Many of these plants, including Bignoniaceae, Lamiaceae and Scrophulariaceae, would simply disappear if bees were suddenly eliminated from the systems in which they occur. Even in many groups characterized by more open pollination systems, such as many Asteraceae, Euphorbiaceae, Rhamnaceae, or Apiaceae, it is likely that pollination interactions and ultimately community structure would be greatly altered in the absence of bees.

As we have indicated in the preceding discussions, different bee taxa are not interchangeable in their role as pollinators because of differences in characteristics such as size, phenology, or resource utilization patterns. Many plants appear to be dependent on very restricted sets of bees as pollinators. Although the common honeybee is sometimes held up as a quintessential pollinator, its widespread use in agronomic systems is due more to the ease with which populations can be manipulated rather than any inherent superiority as a pollinator. Indeed, it is sometimes argued that honeybees and other highly eusocial bees are often in-

effective or even deleterious, in their role as pollinators (Roubik, 1989; Westerkamp, 1991).

As we suggested, current data indicate that there is no clear link between bee and plant species diversity. In many communities it is likely that at least some bee species are ecologically redundant or even irrelevant to the maintenance of effective pollination systems. Nevertheless, given our incomplete knowledge of pollination interactions in all communities, it is exceedingly difficult to see what level of bee diversity is necessary to maintain existing plant diversity. It is likely that from a pollination standpoint, bee diversity may be important even when dealing with bee species that appear to be ecologically equivalent as pollinators. Populations of different bee taxa may be independently regulated by factors other than floral resource availability, such as nest site availability, nest parasites or pathogens, or predators. Diverse arrays of bee species might therefore present a more stable pollinator population, necessary for proper functioning of many successful plant reproductive systems, than would populations of a few or a single bee species. This, of course, is pure speculation. To a very large extent, our understanding of the importance of particular bee taxa, or bee diversity, in pollination systems remains in its infancy. We have touched on only a few of the ways in which different plants are dependent on particular bee species as pollinators. Much work remains to be done, both at the community level and for particular bee-plant interactions to unravel fully the roles of different bees as pollinators in natural communities.

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Diversity of Native Bees and Agroecosystems

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Introduction

Bees are not immune to the biodiversity crisis. This presents us with a serious problem: about 30% of human food is derived from bee pollinated plants (McGregor, 1976). The total value of bee pollinated crops in the United States is about 143 times the value of honey and beeswax and was estimated at US\$18.9 billion (£10 billion) for 1980 (Levin, 1983). These pollination services are now under threat.

Crane (1975) estimated that on a world basis, the value of crops pollinated by bees exceeds the value of the annual honey crop by a factor of 50. There are no figures for the value of crops pollinated by native bees and no reliable figures for the value of all bee pollinated crops in the underdeveloped world.

Pollination by bees involves many more species than just the honeybees. The crops for which honeybee management provides, or is thought to provide, adequate pollination are well documented (Free, 1970, 1976; McGregor, 1976; Martin *et al.*, 1980; Crane and Walker, 1984; Sihag, 1985; Kapil, 1986; Ahmad, 1987). Indeed, honeybees are often considered as ideal pollinators in agriculture: they are easily managed and transportable; they are polyphagous and have a long flight season; it is relatively easy to impose saturation coverage of a crop; and, with their well-known system of communication and aggressive foraging, honeybees can exert a commanding presence among flower-visiting insects.

It is usually presumed that the honeybee, *Apis mellifera*, is the major pollinator of food crops, especially in the overdeveloped world. It has been claimed that this species is responsible for 80% of all pollination (Robinson *et al.*, 1989),

but Kevan *et al.* (1990, quoting Southwick) suggest that the value of honeybees is much lower than this. Any figures for the total value of crops pollinated by honeybees should be regarded with suspicion: figures are based on estimates from apiculturalists, who are either unaware of, or who disregard, the pollination services of native bees.

However, in the United States, according to McGregor and Levin (1970), two-thirds of the land area devoted to insect-pollinated crops was not supplied with honeybee colonies. It follows that much of North American crop pollination is dependent upon the adventive services of managed honeybees, feral honeybees and wild bees. Although the largely unknown factor in the equation is the value of pollination services by wild bees, it is clear that, whatever the value of crops pollinated by native bees, it is clear that agriculture can no longer rely largely on one species, the honeybee, for its pollination services (Torchio, 1987, 1990b).

The aims of this chapter are to:

1. review examples where honeybees are not the ideal or optimal pollinators;
2. highlight crops for which native bees are, or are potential, major pollinators, either alone, or as adjuncts to honeybees;
3. highlight areas where concern for biodiversity and its conservation impinges directly on economically important pollination systems;
4. demonstrate that native bees are in decline in many parts of the world;
5. suggest suitable conservation measures;
6. outline and discuss areas of further study and recommend ways of improving our understanding of native bees as pollinators.

For the purposes of this chapter, the term 'native bees' refers to any non-*Apis* species, irrespective of whether the bee in question is indigenous to the geographic area under discussion.

Drawbacks in the Use of Honeybees as Major Pollinators

Although for many crops the honeybee will continue to be the managed pollinator of choice, there are circumstances which reduce its efficiency. Westerkamp (1991) summarized these, pointing out that while behavioural flexibility is one of the keys to the honeybee's success, its 'predictable unpredictability' means that, despite the great antiquity of the eusocial Apidae (Michener and Grimaldi, 1988), there are no plant species which are specialized for pollination by it.

Africanized honeybees, which have spread throughout much of the tropical Americas, pose special problems. Their aggressiveness and tendency to abscond from the nest have disrupted the beekeeping and pollination industries in the region (Taylor, 1988; Smith, 1991).

Some examples of situations where honeybees may be poor or suboptimal pollinators are given below.

Epidemica and pandemic disease and parasitization

Too heavy a reliance on honeybees for pollination exposes the grower to the possibility of catastrophic reduction of seed set because of epidemic and pandemic diseases, especially where crops are 'saturated' with honeybees (Robinson *et al.*, 1989). The recent pandemic of varroatosis (infestation with *Varroa* mites) in Israel may have caused losses of the cantaloupe melon crop (*Cucumis melo* L.) (D. Eisikowitch, pers. comm.).

Poor flower-handling ability/efficiency

Honeybees are not efficient pollinators of alfalfa (=lucerne, *Medicago sativa*). Although inexperienced foragers are effective pollinators, they react badly to the 'tripping' mechanism of the flowers and soon learn either to avoid them or to manipulate the flowers in such a way that tripping and therefore pollination do not occur (Robinson *et al.*, 1989).

In North America attempts have been made to breed honeybee strains which are well adapted to alfalfa flowers (Nye and Mackensen, 1968, 1970). However, the honeybee has been largely superseded by the Alfalfa leafcutter bee, *Megachile rotundata*, and the Alkali bee, *Nomia melanderi*, as managed pollinators by alfalfa seed growers (see below).

Honeybees are generalists *par excellence*, with a wide repertoire of behaviours, but buzz pollination is not one of them. This is a means of extracting pollen from poricidally dehiscent anthers, using high frequency 'buzz' vibrations of the flight muscles (Buchmann, 1983). Although honeybees may glean pollen which has been dislodged by other insects from such flowers, they are unable to pollinate them.

The principal crops which require buzz pollination are members of the Solanaceae, such as tomato (*Lycopersicon esculentum*), eggplant (= aubergine, *Solanum melongenum*), potato (*Solanum tuberosum*), and peppers (*Capsicum annuum* and *C. frutescens*) and blueberries and cranberries (*Vaccinium* spp., Ericaceae).

Climatic and temperature limitations on honeybee activity

Many early spring-flowering fruits such as blueberry, early apple varieties and almonds appear when daytime temperatures may barely exceed the threshold temperature for honeybee flight; such crops may be largely dependent on native bees which can fly at lower temperatures (Boyle-Makowski, 1987).

Given sufficient water, crops such as alfalfa (USA) and melons (Israel) will grow in extreme desert conditions which are too hot or dry for honeybees. Here, the costs of providing additional bee forage to sustain apiaries during the non-flowering season of the crop are high and may be prohibitive, especially if the beekeepers have to be compensated for low honey yields.

Economic pressures

The fluctuating price of honey can have adverse effects on the use of honeybees as pollinators. According to Levin (1974), in the period 1970–73, honey prices in the United States increased by 254% while at the same time, the cost of living index increased by 14.5%. During this period, the cost of apples rose by 87% and that of alfalfa seed rose by 161%.

When the price of honey rises at such a relatively high rate, there is a strong disincentive for beekeepers to rent out their colonies for pollination because honey production is a more attractive economic proposition.

A slump in the price of honey can be equally detrimental to pollination. In the late 1980s, the price of honey on both the world and North American domestic market declined to about US\$0.80/kg, compared with an estimated production cost of US\$1.20/kg in Ontario (figures quoted in Kevan *et al.*, 1990). In this economic climate, the number of commercial beekeepers in North America has declined in the past decade.

Kevan *et al.* (1990) pointed out that this decline is likely to continue in the face of two additional threats that now face agriculture in North America, namely the parasitic mites *Acarapis woodi* Renn. and *Varroa jacobsoni* Oued. (Needham *et al.*, 1987). Despite proposed control measures and quarantine procedures, the prediction of Kevan *et al.* (1990) that the latter mite will eventually enter North America, has sadly proved correct (Anon., 1987; Connor, 1987; Southwick, 1987; Tew, 1987). More recently *Varroa jacobsoni* has become established in southern England (Paxton, 1992).

Control measures will inevitably increase the costs of beekeeping, an already labour-intensive enterprise, and apiculture will continue to decline in North America, especially among hobbyists. In the warmer, southern United States, an additional threat looms in the form of the Africanized honeybee (Morrison, 1989). Thus the free pollination services provided by honeybees will also decline.

With crop pollination by honeybees in the United States under threat, the role of native bees assumes greater importance. Varroaosis has already swept through much of Europe and while there are as yet no figures available on the implications for crop pollination, they are likely to be dire. Since the 1980s, the movement of honeybee colonies in Czechoslovakia has been prohibited as an anti-*Varroa* measure, resulting in insufficient pollination in alfalfa-growing areas (Ptáček and Rotrekl, 1990).

Declines in native bee populations are now being widely documented in Europe (see below). It follows that for agriculture in both North America and Eurasia, the need to conserve native bees and study their potential as managed pollinators is now more urgent than ever (Torchio, 1990b; Corbet, 1991; Corbet *et al.*, 1991).

Native Bees as Crop Pollinators: Case Histories

Many reports of native bees pollinating crops are simply records of flower visitation and make the implicit assumption that a visit is the same as a pollination event. Thus the literature is full of anecdote. Nevertheless, there is now a growing realization that for many crops, native bees are either an important adjunct to honeybees as pollinators or are superior to them; their role has been discussed by Batra, (1967, 1977), Atwal (1970), Bohart (1970, 1972) Free (1970, 1976), McGregor (1976), Parker and Torchio (1980), Reddi and Reddi (1984), Sihag (1985), Kapil (1986), Parker *et al.* (1987), Corbet (1991) and Corbet *et al.* (1991). Native bees are also valuable pollinators of horticultural crops (Atwal and Grewal, 1968) and plants of herbal and medicinal importance (Ricciardelli D'Albore, 1983a, 1988).

Bumblebees (*Bombus* spp.) and clover pollination in New Zealand

New Zealand has a small fauna of 23 native solitary bee species, all of which are short tongued. Although the climate and soils are ideal for growing forage crops such as clover (*Trifolium* spp.), the native bees are incapable of adequate pollination and honeybees are poor pollinators of some long-tubed cultivars of clover. Sheep and cattle farmers therefore had to import clover seed from Europe.

In the 1880s, three species of bumblebee were introduced into New Zealand from southern England, namely *Bombus terrestris*, *B. subterraneus* and *B. ruderatus*. The bumblebees became established and within a few years New Zealand was a net exporter of clover seed (Gurr, 1962, 1972). Bumblebee pollinated clover became the basis of cheap dairy produce and meat enjoyed for nearly 100 years by British consumers and which contributed greatly to Britain's post-war recovery.

The New Zealand experience is a good example of how a low diversity of pollinators can fail agriculture. It is ironic that one of the bumblebees introduced to and thriving in New Zealand, *B. subterraneus*, is now very rare in Britain. More recently, *B. ruderatus* has been introduced into Chile for red clover pollination (Arretz and Macfarlane, 1986).

Alfalfa (*Medicago sativa*) and native bees in North America and Eurasia

Alfalfa (lucerne) is an important forage crop for cattle and, as a legume, contributes to soil fertility. It is the fourth most valuable crop grown in North America (Olmstead and Wooten, 1987). Two native bee species are managed as pollinators for alfalfa seed production in the United States.

The alkali bee, *Nomia* (*Acunomia*) *melanderi* (Halictidae) is a gregarious, ground-nesting bee indigenous to the western United States (Moure and Hurd, 1987). Management involves the provision, next to alfalfa fields, of 'bee beds',

Table 7.1. Leguminous forage crops (except alfalfa) for which native bees are or are thought to be the major pollinators.

Crop	Bee species	Family	Country	Reference
Sainfoin <i>Onobrychis viciifolia</i>	<i>Bombus</i> spp.	APIDAE	Italy	Ricciardelli D'Albore and Roscioni (1990)
Sweet clover <i>Melilotus</i> spp.	<i>Anthidium</i> sp.	MEGACHILIDAE	Iran	Tirgari (1967)
	<i>Megachile</i> sp.	MEGACHILIDAE	Iran	Tirgari (1967)
Sunn hemp <i>Crotalaria juncea</i>	<i>Chalicodoma lanatum</i>	MEGACHILIDAE	India	Atwal <i>et al.</i> (1969)
	<i>Chalicodoma lanatum</i>	MEGACHILIDAE	India	Abrol and Kapil (1988)
	<i>Chalicodoma flavipes</i> ¹	MEGACHILIDAE		
	<i>Xylocopa fenestrata</i>	ANTHOPHORIDAE		
	<i>Xylocopa frontalis</i>	ANTHOPHORIDAE	Brazil	Couto <i>et al.</i> (1988)
	<i>Xylocopa griseocens</i>	ANTHOPHORIDAE		
Pigeonpea <i>Cajanus indica</i>	<i>Chalicodoma lanatum</i>	MAGACHILIDAE	India	Atwal <i>et al.</i> (1969)
Birdsfoot trefoil <i>Lotus corniculatus</i> and <i>Medicago arborea</i>	<i>Andrena ovata</i>	ANDRENIDAE	Italy	Ricciardelli D'Albore (1984)
	<i>Stelis signata</i>	MEGACHILIDAE		
	<i>Osmia rufa</i>	MEGACHILIDAE		
	<i>Megachile apicalis</i>	MEGACHILIDAE		
	<i>Megachile leachella</i> ²	MEGACHILIDAE		
	<i>Xylocopa violacea</i>	ANTHOPHORIDAE		
	<i>Anthophora plumipes</i>	ANTHOPHORIDAE		
	<i>Bombus</i> spp.	APIDAE		

Red clover	<i>Trifolium pratense</i>	<i>Bombus pascuorum</i> <i>Bombus lapidarius</i>	APIDAE APIDAE	USSR	Berezin <i>et al.</i> (1987)
Bush clover	<i>Sericea lespedeza</i>	<i>Dialictus</i> (5 spp.) <i>Anthidiellum perplexum</i> <i>Megachile</i> (6 spp.) <i>Chalicodoma</i> (2 spp.) <i>Xylocopa virginica</i>	HALICTIDAE MEGACHILIDAE MEGACHILIDAE MEGACHILIDAE ANTHOPHORIDAE	USA (Alabama)	Cane and Snyder (1986)
Cicer milkvetch	<i>Astragalus cicer</i>	<i>Megachile rotundata</i> <i>Bombus huntii</i> <i>Bombus nevadensis</i>	MEGACHILIDAE APIDAE APIDAE	Canada	Richards (1987)
<i>Crotalaria intermedia</i> and <i>Lotonaris bainesii</i>		<i>Megachile macularis</i> <i>Megachile rhodogastra</i>	MEGACHILIDAE MEGACHILIDAE	Australia	Bray (1968)

¹Presumably a misidentification: *Chalicodoma flavipes* does not occur in India.

²Given as *M. brachella* [sic].

areas of compacted soil, with the means to maintain soil moisture and salinity at levels optimum for the bee (Stephen, 1965).

The alfalfa leafcutter bee, *Megachile (Eutricharaea) rotundata* (Megachilidae) is adventive in the United States and originated in Eurasia (Krombein *et al.*, 1979). Like a great many megachilids, *M. rotundata* is an opportunistic nester in ready-made cavities and this is exploited by alfalfa seed producers; farmers provide drilled 'bee boards' in mobile shelters which they space evenly through the fields. The rearing and distribution of *M. rotundata* on a commercial scale is now a multimillion dollar business in the states of Washington, Oregon, Idaho, Utah and Nevada. The management of *Nomia melanderi* and *Megachile rotundata* for alfalfa pollination is now a classic of applied biology (Bohart, 1972; Bitner, 1979; Johansen *et al.*, 1978, 1982).

Two other species of Eurasian *Megachile* are adventive in the United States and are potentially manageable as pollinators of alfalfa. These are *M. concinna* and *M. apicalis* and are close relatives of *M. rotundata*. Parker *et al.* (1976) found that in experimental cages, *M. concinna* built about four times as many cells as *M. rotundata*, reared more second generation adults and were responsible for a higher seed yield.

Another native bee which is a potential alfalfa pollinator in North America is the ground-nesting anthophorid *Florilegus condignus* (LaBerge and Ribble, 1966).

Parker *et al.* (1987) report an unpublished pilot study of what they call *Chalicodoma mucorea* (Fabricius) (= *Chalicodoma nigripes* (Spinola), T. Griswold and D. Baker, pers. comm.). This bee, which was imported from Egypt, where it is an important pollinator of legumes, has potential for alfalfa pollination in the arid south-western United States. Another species, related to but apparently distinct from *Ch. montenegrense*, is oligolectic on desert legumes in southern Israel and may have potential for alfalfa pollination (O'Toole, unpublished).

Batra (1976) described trials of two Eurasian species, *Anthidium florentinum* and *Pithitis smaragdula* for alfalfa pollination. They were imported from India to the United States; the former has promise for alfalfa pollination in the arid south-west, and the latter may be useful for crops in subtropical areas and in greenhouses. A newly discovered native bee, *Osmia sanrafaelae*, has potential for the pollination of alfalfa in desert regions in North America (Parker, 1985, 1986, 1989). This species, endemic to the San Rafael Desert of Utah, is oligolectic on legumes.

Watmough (1987) found that two native bees, *Megachile gratiosa* and *Xylocopa caffra* were suitable pollinators of alfalfa in South Africa and readily used artificial nests.

Alfalfa originated in the steppes of Eurasia and it is not surprising that there are many reports of indigenous native bees as effective pollinators (Biliński, 1985; Ruszkowski *et al.*, 1985; Dockova *et al.*, 1987; Golikov, 1987; Ricciardelli D'Albore and Canale, 1989). Benedek and Moczar (1972) listed seven native bee species in Hungary which are more efficient pollinators of alfalfa than honey-

bees by virtue of their rate of flower visitation and the amount of pollen they transport. Ricciardelli D'Albore (1983b) discussed the importance of native bees in the pollination of five legume crops in Italy.

Other leguminous forage crops which are pollinated by native bees are outlined in Table 7.1.

Orchard crops

All the standard temperate zone orchard crops require insect pollination for good quality fruit and high yields. Although commercial growers of rosaceous fruits such as almond, apple, apricot, cherry, nectarine, peach, pear and plum use hired honeybee colonies for pollination purposes, yields may be disappointingly low.

There is now a growing body of evidence that native bees are often more efficient orchard pollinators than honeybees (Klug and Bünemann, 1986). Goebel (1988) noted that crops such as papaw, passion fruit, granadilla, mango and grape are more attractive to native bees than to honeybees and cited *Amegilla pulchra* and *Xylocopa bryorum* as the commonest visiting species. Corbet and Willmer (1980) showed that carpenter bees (*Xylocopa* spp.) were very efficient pollinators of passion fruit on the Caribbean island of St Vincent. More recently, in Malaysia, Mardan *et al.* (1991) studied the nesting biology of *Xylocopa* (*Platynopoda*) *latipes* in an orchard of passion fruit and discussed the possible management of this effective pollinator.

In some instances, native bees are valuable because they can forage at lower temperatures than honeybees. Examples are the carpenter bee, *Xylocopa valga* on almonds in Kashmir (Abrol and Bhat, 1989; Abrol, 1990), the mason bees, *Osmia taurus* (Given as *cornifrons*) and *O. pedicornis* on apples in Japan (Maeta and Kitamura, 1965a,b; Kitamura and Maeta, 1969) and the blue orchard bee, *Osmia lignaria propinqua*, on apples and almonds in North America (Torchio, 1987).

Torchio *et al.* (1987) introduced a Spanish population of the Eurasian mason bee, *Osmia cornuta*, into Californian almond orchards where the bees were successful pollinators. A regional subspecies, *Osmia cornuta semirufa*, may therefore have potential as a managed pollinator for almonds in Israel, where there is a particular problem. The local cultivar is not very attractive to honeybees and the nectar, and hence honey, is tainted with the bitter alkaloid amygdalin (D. Eisikowitch, pers. comm.). *O. c. semirufa* is one of 14 species of native bees which visit semi-wild almonds in Israel (O'Toole, unpublished).

Blueberries and cranberries (*Vaccinium* spp.) are increasingly important crops in eastern North America. They have poricidal anthers and depend therefore on vibratile or 'buzz' pollination. As a consequence, honeybees are inefficient pollinators (see above). A wide range of native bees are pollinators, including species of *Colletes*, *Andrena* and *Bombus* (Finnamore and Neary, 1978). In the south-eastern United States, *Emphoropsis laboriosa* (Anthophoridae) is oligolectic on blueberries, especially *Vaccinium ashei* and *V. corymbosum*

(Cane and Payne, 1988, as *Habropoda laboriosa*). This species has a flower visiting rate which is three times that of species of *Bombus*.

Although growers of blueberries and cranberries have always relied on the services of unmanaged native bees (Schrader and LaBerge, 1978), Batra (1980) was able to use synthesized linalool, the mandibular secretion of three related and sympatric species of *Colletes*, to induce nesting in a specially prepared sand bed. One of these species, *Colletes validus* Cr., is oligolectic on *Vaccinium* and the use of pheromones in the management of native bees is a promising development. More recently, Torchio (1990a) reported on the management of *Osmia ribifloris biedermannii* for the pollination of highbush blueberry in southern California.

A selection of other crops for which native bees are or are likely to be the major pollinators are listed in Table 7.2.

Management of bumblebees (*Bombus* spp.) for pollination

There is a wealth of literature on the role of *Bombus* species as pollinators of crops, especially clover (Free, 1970, and references therein; Pouvreau, 1984; Plowright and Laverty, 1987).

Techniques for the managing of colonies for the pollination of field crops were given by Holm (1966), Plowright and Jay (1966), Fridén (1967), Palmer (1968), Valle and Aaltonen (1969), von Hagen (1988), Marletto *et al.* (1988), Griffin and Macfarlane (1990) and Macfarlane *et al.* (1991).

Honeybees perform badly under glasshouse conditions. Bumblebees, by contrast, adapt well and *Bombus terrestris* is used in Holland for the year-round pollination of tomatoes (van Ravestijn and van der Sande, 1991) and aubergines. Associated with this is a growing literature on the techniques of establishing and managing colonies for use in glasshouses (e.g. Heemert *et al.*, 1990; van den Eijnde, 1990; Duchateau, 1991). There is also current research in Israel on the management of glasshouse populations of *B. terrestris* for the pollination of tomatoes (A. Hefetz, pers. comm.). Velthuis and Cobb (1991) reported on the use of bumblebees in the production of seeds of *Primula obconica* in a greenhouse setting.

Native Bees in Decline

Modern, intensive agribusiness, with its emphasis on capital return, has little place for wild areas, marginal land and tracts of natural vegetation. Habitat destruction means a reduced diversity of forage plants and fewer nest sites; it is therefore a major cause for the apparent decline in the diversity and numbers of wild bees. This and the use of insecticides and biocides must be a matter of concern for all with an interest in crop pollination.

While the literature on the use of managed native bees for pollination is

Table 7.2. Examples of crops for which wild bees are either a useful adjunct to honeybees (*) or are superior to them (†) as pollinators.

Crop	Bee species	Family	Country	Reference
Apple <i>Pyrus malus</i>	* <i>Andrena haemorrhoa</i>	ANDRENIDAE	Belgium	Jacob-Remacle (1989)
	* <i>Andrena scotica</i> ¹	ANDRENIDAE		
	* <i>Osmia</i> sp.	MEGACHILIDAE		
	* <i>Anthophora</i> spp.	ANTHOPHORIDAE	Japan	Kitamura and Maeta (1969)
	† <i>Osmia taurus</i> ²	MEGACHILIDAE		
	† <i>Osmia pedicornis</i>	MEGACHILIDAE		
Guava <i>Psidium guajava</i>	* <i>Lasioglossum</i> sp.	HALICTIDAE	Costa Rica	Hedström (1988)
	* <i>Xylocopa</i> sp.	ANTHOPHORIDAE		
	* <i>Bombus mexicanus</i>	APIDAE		
	* <i>Trigona</i> sp.	APIDAE	Australia	Heard (1987, 1988)
	† <i>Trigona</i> spp.	APIDAE		
Macadamia <i>Macadamia integrifolia</i>	† <i>Melipona eburnea</i> ³	APIDAE	Brazil	Peters and Vasquez (1986/87)
Camu-camu <i>Myrciaria dubia</i>	† <i>Scaptotrigona postica</i> ⁴	APIDAE		
Peanut <i>Arachis hypogaea</i>	* <i>Megachile mendica</i>	MEGACHILIDAE	USA	Leuck and Hammons (1969)
	* <i>Lipotriches microsoma</i> ⁵	HALICTIDAE		
	* <i>Megachile ekuivella</i>	MEGACHILIDAE		
Tephrosia <i>Tephrosia vogelli</i>	† <i>Xylocopa brasilianorum</i>	ANTHOPHORIDAE	Puerto Rico	Martin and Cabanillas (1970)
Lowland coffee <i>Coffea canephora</i>	† <i>Creightonella frontalis</i>	MEGACHILIDAE	Papua New Guinea	Willmer and Stone (1989)
Cardamom <i>Elettaria cardamomum</i>	* <i>Amegilla sapiens</i>	ANTHOPHORIDAE	Papua New Guinea	Stone and Willmer (1989)

¹ Given as *A. sabulosa*.

² Given as *O. cornifrons*.

³ Given as *M. fuscopillara*.

⁴ Given as *Trigona portica*.

⁵ Given as *Nomia*.

dominated by a strong North American bias, that which documents the decline of native bees is distinctly Eurocentric. Westrich (1985, 1989a,b) drew attention to the general decline in the wild bee fauna in Germany. It is alarming that several native bee species which are known to be valuable pollinators of alfalfa in central and eastern Europe appear to be in decline or locally extinct. Species such as *Rhophitoides canus* (Halicidae), and *Melitturga clavicornis* (Andrenidae) are on several Red Data Book lists (Day, 1992).

Peters (1972) cited changes in drainage patterns as a cause of decline in bumblebee populations in Germany via a loss of forage plants; the removal of marginal land and hedgerows is also implicated.

Williams (1986, 1988, 1989a,b) described and discussed the notable decline of long-tongued bumblebees in Britain, attributing this to the destructive effects of intensive agriculture. Sims (1984) discussed the same phenomena as they affect beekeeping in Britain, and Gusenleitner (1986) discussed the situation in Austria.

According to Grebennikov (1972), in the 40 years preceding 1972, bumblebees in the Soviet Union declined 'by 300 times'. Declines in bumblebees are recorded from Germany by Donath (1985), who attributes this to various causes, including the poisonous nectar of lime trees and road casualties caused by heavy traffic on roads which traverse flight lines (Donath, 1986, 1988, 1989a,b).

Ruszkowski *et al.* (1988) found that the diversity and abundance of bumblebees was reduced in agricultural areas of Poland where insecticide applications were a regular practice; diversity and abundance were higher in protected areas. Celli and Molle (1984) reported a similar decline in native bees, honeybees and syrphid flies in Italy, attributing the main causes to insecticides and industrial pollution. The injurious effects on bumblebees of metal pollution from a non-ferrous metal works in Poland were documented by Kosior and Nosek (1987), and Kosior (1987) discussed the general impact of 'economic development' on Polish bumblebee populations, citing, in order of seriousness, increases in vehicular traffic and the 'improvement' of meadows.

Fye (1972) discussed the effects of forest disturbance on native wasps and bees in Canada. Both Gauld *et al.* (1990) and Day (1992) and references therein cited many examples and discussed the decline of aculeate Hymenoptera, including bees, and reviewed their conservation needs.

Although there is much evidence of a decline in the diversity and abundance of native bees, there are relatively few accounts of any direct effects on the pollination of economically important plants. Al-Tikrity *et al.* (1970) cited the need in North America to saturate fields of Crown Vetch (*Coronilla varia*) with honeybee colonies because native bee populations were inadequate. Benedek (1972) suggested that weed control measures around alfalfa fields in Hungary had adverse effects on native bees.

In 1973, an accidental application of insecticide in Washington State killed sufficient Alkali bees, *Nomia melanderi*, to incur an estimated loss in alfalfa seed production worth US\$287 000 (Johansen, 1977).

Kevan and LaBerge (1979) described how native pollinators of blueberries in New Brunswick were adversely affected by a change from DDT to fenitrothion used to control Spruce Budworm (*Choristoneura fumiferana*) in adjoining forest. Despite the importation of honeybees to the blueberry orchards to offset the loss of native bees, the growers experienced a decline in yield of 665 tonnes/year (Kevan and Plowright, 1989). This is not surprising: this ericaceous crop depends on buzz pollination, which, as discussed earlier, is not in the behavioural repertoire of honeybees. These authors reported that the use of fenitrothion caused a decline in native bee populations in Quebec and Ontario as well as in New Brunswick.

Field size is another factor which can affect adversely the success of pollination by wild bees. The current and widespread practice of growing monocultures in large fields can reduce seed yields in the central areas of the crop. Stephen (1955) attributed the drop in yield of alfalfa seeds from 1000 kg/ha to 150 kg/ha to land clearance and the consequent loss of nesting sites for native bees. Kevan *et al.* (1983) stated that large-scale monoculture of cranberries may suffer poor pollination and Kevan *et al.* (1990) listed crops such as cocoa, cashews and North American papaw which may suffer in the same way. Pawlikowski (1989) showed that in north-eastern Poland there was an inverse relationship between field size and bee diversity.

Conservation Measures for Native Bees

The importance of native bees for crop pollination makes it imperative that conservation measures are implemented as widely as possible. The agricultural extension services of colleges and research stations around the world should seize the opportunity to educate farmers and growers about the role of native bees in their livelihoods and how to conserve and manage them. Such considerations led Banaszak (1990) to call for the legal protection of 443 species comprising the native bee fauna of Poland and no doubt similar initiatives will follow in other countries.

Transnational organizations such as the European Economic Community, with their increasingly centralized approach to conservation issues, should be encouraged to play key roles in formulating bee-friendly policies.

Habitat conservation/improvement

Much of the decline in diversity of native bee faunas outlined above is the direct result of habitat destruction and reduced floral diversity. Areas of marginal land should be protected and managed to improve the diversity of forage plants.

Tanács and Gulyas (1986) described the importance for native bees of a rich grassland flora associated with river banks in Hungary. Tanács (1987) reported on the beneficial effects of managing dam slopes for increased floral diversity.

The native bee flora varied from 37 to 112 species at ten sampling sites.

Riemann (1987a) found that even the relatively small area represented by the slopes of drainage ditches supported 59 species of native bees in an area of intensive agriculture in a marshy area of Germany. The same author reported that areas of inland dunes are an important reserve for wild bees, forming island reserves which support 96 species of wild bee (Riemann, 1987b). Lukáš (1987) discussed the importance of a refuge which supports 213 native bee species surrounding the town of Trenčín in Czechoslovakia. Scott-Dupree and Winston (1987) argued that uncultivated areas are important reservoirs of native pollinators for orchard crops.

In pear and plum orchards in the Mae Hae region of northern Thailand, Boonithee *et al.* (1991) found that the rates of floral visitation by three wild honeybee species, *Apis cerana*, *A. dorsata* and *A. florea* and stingless bees (*Trigona* spp.), were inversely correlated with the distance from nest sites in the forest. They noted that the use of fire to clear forest had an adverse effect on wild bees and recommended the protection of, or provision of, nest sites.

In studies of native bees as pollinators in Poland and lowland Rumania, Banaszak (1983, 1985) and Banaszak and Manole (1987) recommended that about 25% of land in the 'agricultural landscape' – forests, meadows and roadside swards – should be set aside and managed as refuge habitats.

With a small-scale version of this approach, Ptáček and Rotrekl (1990) were able to increase the populations of *Rhophitoides canus* in alfalfa fields in Czechoslovakia. They provided strips of bare soil in the crop as nesting sites. During the first cut, they left strips of untouched alfalfa as a source of food for the bees. They also maintained a bee-friendly programme of pesticide applications, using compounds relatively harmless to bees and appropriate timings of applications.

Rhophitoides canus is one of the most efficient pollinators of alfalfa and the impetus for this work arose from the current prohibition in Czechoslovakia on the movement of honeybee colonies as an anti-*Varroa* precaution. This is the first time populations of this ground-nesting halictid have been actively managed for pollination purposes.

Batra (1982), Kevan *et al.* (1990), LaSalle (this volume Chapter 8) and Altieri *et al.* (Chapter 11) point out that refuge areas have other advantages in that they provide havens for insect parasitoids which are beneficial in the biocontrol of pests.

Discussion

Anyone who has read John Steinbeck's novel *The Grapes of Wrath* or who has flown over Nebraska and Kansas, knows that the biodiversity crisis started a long time ago; it is now well under way in areas under intense, modern agriculture. We have witnessed what Harlan (1971) has called 'genetic wipe-out'. Non-

sustainable logging and clear-felling are having the same effects in tropical rain forests (Wilson and Peter, 1988).

A frequently cited justification for rain forest conservation is the presumed wealth of secondary plant compounds which await exploitation as drugs (Farnsworth, 1988). We need to regard the still largely unexplored fauna of native bees as an untapped resource of equal importance.

Rain forests, though, are not notably rich in bees. The greatest diversities are in semi-arid and temperate deserts (Michener, 1979; O'Toole and Raw, 1991). Unfortunately, fragile desert habitats are often overlooked as the debate on biodiversity and its conservation focuses on rain forests.

We cannot feed everyone on this planet: about 1 billion people, one-fifth of the world's human population, is undernourished at the present time. It is imperative, therefore, that we conserve our native bees as a pool of potentially manageable pollinators for crops. If we are to make the best use of the free ecosystem services provided by native bees, then we need much more research in a variety of subject areas. Kevan (1991) discussed the importance of pollination in both natural systems and agriculture and surveyed the current threats to sustainable productivity.

Recommendations

Conservation is not enough. If we are to make the most of our native bee faunas, then we need concerted and co-ordinated research efforts in pollination ecology at the community level, a proactive approach to biological inventories and basic bee taxonomy. As Estes *et al.* (1983) pointed out, we need also to improve the communication and synergism between pollination biologists working in the theoretical and applied fields.

Community studies

Neff and Simpson (this volume Chapter 6 and references therein) outline the importance of native bees in the maintenance of plant diversity and natural ecosystems. They point out that studies at the community level of the dynamics of plant-pollinator interactions are still in their infancy. The study by Silberbauer-Gottsberger and Gottsberger (1988) on the pollination of *cerrado* plants in Brazil and the survey of a bee pollinated plant community on beach dunes, also in Brazil (Gottsberger *et al.*, 1988), are good examples of the kind of work required in all biogeographical regions. Such studies are vital in providing fundamental information which may enable us to identify pollination systems and/or pollinators which may be modified for agricultural purposes.

Ignorance of pollination systems can be expensive and may undermine crop production. In the case cited above, it was a useless exercise for the blueberry growers of New Brunswick to import honeybee colonies to offset the dearth of

native bees resulting from inappropriate insecticide use.

West Indian Cherry (Barbados Cherry, Acerola, *Malpighia glabra*) is the richest natural source of vitamin C. It was introduced to Hawaii, where fruit set was poor, even when beehives were moved into the orchard (Yamane and Nakasone, 1961). At the time it was not known that *M. glabra* is dependent on co-adapted, oil-collecting bees for pollination. In the West Indies, the solitary ground-nesting anthophorid bee, *Centris dirrhoda*, is the most effective pollinator (Raw, 1979). Sedgley and Griffin (1989) emphasized that a proper understanding of pollination biology is essential in agroforestry, especially where tree species are removed from the environment where pollination systems evolved.

The proactive approach to native bees and crop pollination

The use of native bees as pollinators, cited above, was originally either fortuitous (e.g. adventive *Megachile rotundata* in the USA) or 'reactive', that is, the seeking of solutions to pollination problems *after* a crop has been developed or introduced into a new region (e.g. *Nomia melanderi*).

Given the problems posed by the biodiversity crisis, a 'proactive' approach is clearly desirable. That is, we need to make biological inventories of our native bee faunas, just as we survey resources such as oil and mineral deposits.

The USDA Bee Biology and Systematics Laboratory at Logan, Utah is virtually the only agency which adopts a proactive approach to native bees and pollination in agroecosystems. Here, USDA scientists survey local bee faunas for nesting biology and floral relationships. They rear and study suitable candidates in a laboratory setting before field trials commence. Parallel with this approach is research on the basic taxonomy of bees and, to this end, USDA maintains an internationally important reference collection of bees.

If we are to address the problems of native bee diversity and pollination in agroecosystems, then ideally, we need bee biology and systematics laboratories on the Logan pattern in all continents. The Mediterranean basin, with its rich bee fauna still not fully surveyed, is a prime candidate. A bee laboratory in this region would have a major role not only in the study of pollination and bee systematics but also in education, sharing skills with scientists from underdeveloped countries. In this region, only Correia (1991), has adopted the Logan proactive approach, with a survey of native bees as potential pollinators.

Fussell and Corbet (1991) showed that it is possible to stimulate public awareness of the need to know more about native bees. They described a national survey of bumblebees in Britain organized by the children's environmental club WATCH, which provided useful information on distribution and flower visitation.

Two other enterprises can serve as models for the future. The Programa Cooperativo sobre la Apifauna Mexicana (PCAM) is a co-operative venture between North American bee scientists and Mexican biologists. The aims are to survey the native bees of Mexico, their floral relationships and nesting biologies,

to create a reference collection of bees in Mexico and to train local scientists in bee taxonomy (LaBerge, 1991).

The Ecoratio project in Israel is a long-term study of the pollination biology of the native flora, comparing the Mediterranean and desert floras. Data on bee-flower relationships and size modalities in bees are being added to an extensive, pre-existing database of the Israeli flora (Shmida and Ritman, 1985). The project involves interactions between botanists, game theorists and bee specialists (O'Toole, 1991).

Basic taxonomy

None of the above prescriptions is meaningful without taxonomy. This is basic to all biological research, yet it continues to be the Cinderella of biology so far as the allocation of resources is concerned; even among biologists, taxonomy continues to be undervalued (Fosberg, 1972; Danks, 1988). In the rare cases where adequate funding is available, a lack of suitable personnel can be a problem: Dourojeanni (1990) cited the case of a World Bank grant of \$7 million, made in 1982, for a biological inventory of Rondonia and the northern Matto Grosso in Brazil; six years later, 47% of the funds were not spent and little of the work had been completed, largely because of a lack of insect taxonomists.

We need, therefore, to raise the profile of taxonomy and promote taxonomic training not only as a cost-effective investment in the future, but also a very cost-effective form of aid to underdeveloped countries. Because of their ecological and economic importance, bees, together with parasitic Hymenoptera, must be a target group for future training and research.

Recognition of the importance of biodiversity and taxonomy is not new. Out of 66 'scientific' bee species, the Kayapó Indians of Amazonian Brazil recognize 56 'folk' species (Posey, 1982; Posey and Camargo, 1985). By the age of 12, a Yãnomamö boy can recognize about 20 species of stingless bee (*Trigona* spp.), using structural, behavioural and nest architecture characters (Chagnon, 1968). We can achieve such feats only with the aid of literature, reference collections and a microscope. These Amerindians have an understanding of biodiversity and taxonomy which is adequate for their needs. Ours is not. We have much to learn from these advanced people.

A note on bee nomenclature

The names of bee species used in the text and tables are those given in the cited literature and their use here does not imply validity; where cited names are known to be invalid, the correct name has been indicated.

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Parasitic Hymenoptera, Biological Control and Biodiversity

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Introduction

Parasitic Hymenoptera represent the most species-rich group of Hymenoptera, and one of the most speciose of all insect groups. They are common and abundant in all terrestrial ecosystems. Although a variety of biologies are known, species generally develop as parasitoids of a wide range of other insects. Repeated biological control successes have proven that hymenopterous parasitoids can play a crucial role in pest population regulation and, by extrapolation, suggest that they have an equally important role in the natural regulation of populations of phytophagous insects. The large number of parasitic Hymenoptera species, combined with their ability to respond in a density-dependent manner to the population size of their hosts, makes them essential to the maintenance of ecological balance and a contributing force to diversity in other organisms (LaSalle and Gauld, 1992).

'Parasitic Hymenoptera' is not a precise term, and is presently not adequately defined either taxonomically or biologically. The *Parasitica* is a taxonomic category which represents one of the two major divisions of the *Apocrita*. However, not all members of the *Parasitica* are parasitic, and there are many *Aculeata*, and even some *Symphyta*, which have a parasitic lifestyle (see LaSalle and Gauld, this volume Chapter 1). The rationale put forward in this chapter for the importance of parasitic Hymenoptera applies equally well to any of the hymenopterous parasitoids. Members of the aculeate superfamily *Chryridoidea* are parasitic, and the *Bethylidae* in particular have many aspects of their biologies which are very similar to species of *Parasitica*. For the purpose of this

chapter, the term parasitic Hymenoptera can be considered to apply to any hymenopterous parasitoid. And despite any difficulties in defining this group, the vast majority of Hymenoptera are parasitoids.

It is probable that at least 75% of parasitic Hymenoptera species have yet to be described, and that many of those that are currently described are not recognizable (LaSalle and Gauld, 1992). Parasitic Hymenoptera are even more poorly understood biologically than taxonomically. Although a good deal of biological or ecological information is known for some species (see, for example, Clausen, 1940; Askew, 1971; Waage and Greathead, 1986), there are many genera, and even a few of the smaller families, which are known only from a minimal amount of collection information. Taxonomic knowledge alone will not serve to protect species; basic biological, behavioural and ecological information is necessary to any attempt to ensure their survival.

Parasitic Hymenoptera and Biological Control

There are two reasons why it is imperative to consider biological control when discussing parasitic Hymenoptera. The first is that parasitic Hymenoptera are clearly the most important group of biological control agents, and responsible for the majority of the substantial economic and environmental benefits which are produced through biological control programmes. The second is that information gained from biological control studies can provide insights into other disciplines, such as conservation biology, and much of this information may not be available from any other sources.

An important attribute of many parasitic Hymenoptera, particularly in regard to their ability to provide effective biological control, is that they react to the population size of their host in a density-dependent manner (Huffaker and Messenger, 1964; Huffaker *et al.*, 1976, 1984). The intensity of their mortality producing actions increases with an increase in host population, and relaxes with a decrease in host population. In this manner, the two linked populations fluctuate between certain upper and lower limits that prevent both a massive increase in the host population size and a decrease to the point of extinction.

It is difficult (if not impossible) to measure the actual degree of control that parasitoids which operate in a density-dependent manner exert in undisturbed natural systems; however, one can directly observe and measure the regulatory abilities of parasitoids used in biological control projects (DeBach *et al.*, 1976; Huffaker and Gutierrez, 1990b). The results of such tests provide evidence that parasitic Hymenoptera are more extinction prone than their herbivorous hosts, and some indication of the possible cascade effects that could result from the loss of parasitic Hymenoptera species.

Parasitic hymenoptera as biological control agents

Parasitic Hymenoptera are the most important single group of biological control agents. Greathead (1986) showed that parasitoids have been established more than twice as often as predators in biological control importations, and have been effective in the same ratio. He listed 393 species of parasitoids established in classical biological control programmes, of which 344 (87%) were parasitic Hymenoptera, and hymenopterous parasitoids were responsible for providing effective biological control in the same ratio (Greathead, 1986: Table VII).

The economic savings due to parasitic Hymenoptera are substantial. Dean *et al.* (1979) reviewed the control of the rhodesgrass mealybug, *Antonina graminis* (Homoptera: Pseudococcidae), by the encyrtid *Neodusmetia sangwani*. The total funding for this project, which was handled by the Texas Agricultural Experimental Station at Weslaco (TAES), was less than US\$200 000; the estimated cost benefit ran to several hundred million dollars. Economic savings to the state of Texas for one year alone not only greatly exceeded the cost of the project, they surpassed the total of all operational funds spent on the TAES in the 65 years from its founding in 1923 until the paper was written in 1978.

Norrgard (1988a,b) showed the benefit-cost ratio for the control of cassava mealybug (*Phenacoccus manihoti*) by the encyrtid *Epidinocarsis lopezi* in Africa to be 149 to 1, with annual savings as high as US\$250 million. The savings to California agriculture due to seven major biological control successes are around US\$250 million (van den Bosch *et al.*, 1982). They based their figure only on savings in crop losses and insecticide applications, thus it may be conservative because it does not take into account possible increases in pest distribution which would occur in the absence of biological control agents. However, the economic considerations of biological control are perhaps less important than the environmental savings due to decreased pesticide usage.

DeBach and Rosen (1991) discussed many similar biological control successes involving parasitic Hymenoptera. These include: purple scale in California, walnut aphid in California, Oriental fruit fly in Hawaii, citriculus mealybug in Israel, coconut leaf-mining beetle in Fiji, spiny blackfly in Japan, citrus blackfly in Cuba, cereal leaf beetle in the United States, Alfalfa blotch leafminer in the eastern United States, woolly whitefly in California and elsewhere, Comstock mealybug in the Soviet Union, as well as projects which involve parasitic Hymenoptera in conjunction with other natural enemies.

These projects provided (and continue to provide) not only the economic and environmental benefits associated with biological control, but also direct evidence for the ability of parasitic Hymenoptera to regulate the populations of other insects.

Parasitic hymenoptera diversity and biological control

The presence of a high level of diversity of parasitic Hymenoptera can be thought of as having potential value or actual value to biological control projects.

Diversity which is conserved in natural systems is available as a potential resource to biological control projects; the variety of organisms which have been introduced and established against any given pest have an actual value in the control they provide. This section discusses the importance of such diversity to biological control; the complexity within Hymenoptera parasitoid communities in agroecosystems, and ways to enhance parasitic Hymenoptera diversity are discussed by Altieri *et al.* (This volume Chapter 11).

Natural parasitic Hymenoptera diversity as a biological control resource

Waage (1991) has already pointed out the strong link between the subjects of biological control and biodiversity. It is fundamentally important to conserve a large reservoir of natural parasitoid diversity, regardless of what we know about the taxonomy or biology of that reservoir, because we cannot predict which species might become pests in the future. Sailer (1983) estimated that 11 potential pests enter the United States every year, of which seven are liable to be injurious. A variety of new pests could also be created through changing agriculture and forestry practices through developing areas of the world. Maintaining the ability to control tomorrow's pests in a manner that is both economically and environmentally sound is one of the strongest arguments for preserving biodiversity.

Naturally occurring parasitoids of any given pest (or potential pest) are important not only to that pest. Parasitoids have been known to switch over from a native host to a related introduced host, sometimes with striking results. The whitefly pest *Parabemisia myricae* was first discovered in California in the late 1970s, where it had probably been introduced from Japan (DeBach and Rose, 1982; Rose and DeBach, 1992). Two species of parasitoids were imported from Japan as natural enemies of this whitefly, and became established in various regions. However, the most successful control agent proved to be a previously unnoticed Californian species, subsequently named *Eretmocerus debachi* (Aphelinidae), which switched over onto *P. myricae* from its native host to provide substantial control (Rose and DeBach, 1982, 1992). All three parasitoids were later shipped to Israel as control agents against an invasion of *P. myricae* in that country. It was the California parasitoid rather than the Japanese ones, which were naturally occurring parasitoids of *P. myricae*, which provided complete control in Israel (Swirski *et al.*, 1987, 1988; Rose and DeBach, 1992). *Eretmocerus debachi* has subsequently been imported to Turkey, where it has again provided complete control of *P. myricae* (Uygun *et al.*, 1990; Rose and DeBach, 1992).

Diversity of parasitic Hymenoptera within biological control programmes

The number of imported natural enemies used in any project can be important; a high diversity of imported biological control agents can be a contributing factor

to the degree of success. If different species are more effective at different times of year, or on different host plants, or at different population densities, or at the same time but on different host life stages, or in any other way complement each other to produce a higher level of control, then diversity is important. Introduction strategy in biological control has been a controversial subject through the years, and one of the centres of debate concerns the introduction of single versus multiple species of natural enemies. Although this chapter takes the view that the introduction of more than a single species is desirable, a review of the subject with a list of representative references expressing diverse viewpoints is given by Ehler (1990).

Huffaker (1971: 61) summed up the value of multiple species introductions by saying, 'Importation of a diverse complex of natural enemies is the only practical manner of obtaining the best species for a given habitat, or the best combination for such habitat, or the best combination for the entire host range'. DeBach and Rosen (1991) gave several reasons why the introduction of more than a single species of natural enemy is beneficial to biological control projects.

1. Multiple importations are the only practical manner of obtaining the best natural enemy, or combination of natural enemies, for a given habitat or host range.
2. Competition between various species of natural enemies is not normally detrimental to overall host population regulation; the displacement of any given species usually means that the second is more effective and will produce greater control. Competing populations of natural enemies may affect each other's individual efficiency, however their combined effect on the host population will be greater.
3. Although there is usually one best natural enemy for any particular habitat, climate, or host stage, it might require additional species to provide control throughout the entire geographic and climatic range, or life cycle, of a pest.
4. The best natural enemy may not be found until all natural enemies are known.

Evidence that the best species might not have been the one which would have been originally selected for the task can be found in the discussion of *Parabemisia myricae* above, where the most effective parasitoid turned out to be not from the native home of the target pest, and not even originally a parasitoid of the target pest. Clearly, this is not a species which would have been ranked highly for importation in this case.

Additional support for the idea of introducing more than a single species of natural enemy for any given pest is supplied simply by observing host/parasitoid relationships in nature. Phytophagous insects are rarely attacked by a single species of parasitoid, but rather by an assemblage of parasitoids (Hawkins and Lawton, 1987; Memmott and Godfray, this volume Chapter 9; Hawkins, this volume Chapter 10). A basic understanding of the manner in which these parasitoids co-exist is thus important to biological control workers (Miller and Ehler, 1990, and references therein).

Hyperparasitoids: the addition of a trophic level

Although a high diversity of natural enemies at the primary trophic level can be advantageous in biological control projects, not all parasitic Hymenoptera are considered beneficial. Hyperparasitoids are parasitoids at advanced trophic levels, that is parasitoids which use other parasitoids as their hosts rather than phytophagous hosts. Nearly all hyperparasitoids are Hymenoptera, and hyperparasitism has evolved independently (from parasitism) in six different superfamilies of the Parasitica (Gordh, 1981). Hyperparasitoids can disrupt and reduce the regulatory ability of parasitoids used in biological control projects, and because of this incoming shipments of parasitoids are carefully screened in quarantine to remove any possible hyperparasitoids.

Despite this, there is some indication that the negative influence of hyperparasitoids on biological control might have been overemphasized (see Bennett, 1981; Luck *et al.*, 1981). Most agroecosystems are not natural, and are relatively species poor. This can lead to instability and large fluctuations in the population size of the host and the parasitoid. Extreme fluctuations can result in the local extinction of the parasitoid, with a subsequent resurgence in population size of the host. Adding a species in another trophic level to this system (hyperparasitoid) may serve to dampen the fluctuations, allowing all species to exist in a more stable system. This might result in a slightly higher population level of the pest, but if this level is more stable, and still below the level of economic damage, the system might benefit. Luck *et al.* (1981) suggested that under certain conditions the presence of a hyperparasitoid might actually improve a biological control system by changing it from one which displayed periodic pest outbreaks to one of continuous subeconomic pest population level.

Facultative hyperparasitoids are parasitoids which can act either as a primary parasitoid, or as a hyperparasitoid of one or several primary parasitoids. The role of facultative hyperparasitoids in biological control has also been questioned. May and Hassell (1981) felt that facultative hyperparasitoids will act dynamically in the same manner as competing primary parasitoids, and as such are candidates in multiple introduction programmes. Ehler (1979, 1990) pointed out that a facultative hyperparasitoid could be of value in a biological control programme under two conditions.

1. The collective impact on host density (by the facultative hyperparasitoid and the primary parasitoid(s) in the guild) is greater than that obtained in the absence of the facultative hyperparasitoid.
2. The facultative hyperparasitoid does not have a significant impact outside the target system (that is on other parasitoid guilds).

Indeed, facultative hyperparasitoids have already been used successfully in biological control programmes. *Oomyzus* (= *Tetrastichus*) *sokolowskii* (Eulophidae) will attack both the diamondback moth (*Plutella xylostella*: Plutellidae) and its braconid parasite *Cotesia* (= *Apanteles*) *plutellae*. Cock (1985; as *Tetrastichus sokolowskii*) reported that *O. sokolowskii* had been intentionally intro-

duced into several areas in the Caribbean, where at times it had achieved high levels of parasitism (up to 68–100% in Barbados in 1976). Both *C. plutellae* and *O. sokolowskii* were subsequently shipped to the Cape Verde Islands, where their combined activity, coupled with other pest management practices, resulted in satisfactory suppression of *P. xylostella* (Cock, 1985).

Walter (1983a,b) discussed divergent male ontogenies and heteronomous hyperparasitoids in the Aphelinidae (Chalcidoidea). In some members of this family males develop in a different manner than females. In these species which display divergent male ontogenies, females are always internal parasitoids of homopteran hosts, while males can develop as external parasitoids of the same host or as internal parasitoids of Lepidoptera eggs or as external hyperparasitoids of aphelinids, encyrtids, or eulophids which are attacking their homopteran hosts. These latter species are known as heteronomous parasitoids, and in some cases the males even develop on females of their own species. The role of heteronomous hyperparasitoids was also examined by Hassell *et al.* (1983). They felt that an interaction with host, parasitoid, heteronomous hyperparasitoid was significantly more stable than an equivalent host, parasitoid, hyperparasitoid interaction, and that parasitoids with deviant male ontogenies may stabilize both their own populations and the communities to which they belong.

The above section concerning hyperparasitoids is not an attempt to justify the intentional importation of hyperparasitoids for use in biological control projects; it is presented to illustrate how additional trophic levels of parasitic Hymenoptera diversity within a managed agroecosystem might not always be detrimental, and might even result in a lower overall pest damage through time or greater stability of the system. As Luck *et al.* (1981:41) pointed out, '... the deleterious impact of a hyperparasite on applied biological control remains to be documented'. However, for an opposing viewpoint see Altieri *et al.* (this volume Chapter 11), who point out that the diversity and abundance of primary parasitoids can be greatly reduced by hyperparasitoids, and the presence of hyperparasitoids can reduce the chances of successful establishment of parasitoids in colonization attempts.

Parasitic Hymenoptera in Natural Ecosystems

Evidence that parasitic Hymenoptera are integral to most terrestrial ecosystems includes: their involvement in trophic interactions; their ability to exert a regulatory effect on their hosts; and presence of keystone species with the predicted cascade effect that their removal would cause.

Trophic interactions

An indication of the fundamental importance of parasitic Hymenoptera is found in the large number of trophic interactions they represent in terrestrial eco-

systems. Hymenopterans account for just over 75% of all insect parasitoids (Eggleton and Belshaw, 1992: Table 2), and parasitoid food chains (chains comprising green plants, insect herbivores and insect parasitoids) contain over half of all known species of metazoans (Price, 1980; Strong *et al.*, 1984; Hawkins and Lawton, 1987). Hawkins and Lawton (1987) examined parasitoids associated with phytophagous insect species in Britain (285 species, in 42 families, in six orders). According to May (1988), their data indicate that a typical phytophagous species is attacked by 5–10 species of parasitoids and that this same pattern holds for phytophagous species in the tropics. A further examination of causes and constraints of parasitoid diversity is given by Hawkins (this volume Chapter 10).

Schoenly (1990) provided a study on the predation of insects, in which he included parasitism within the category of predation. Hymenopterans as predators and parasitoids interact with more numbers of insect prey than any other insect order in terrestrial habitats. He listed 584 Hymenoptera links, followed by 340 for beetles, 51 for bugs and 32 for flies; Hymenoptera were responsible for over half (57%) of all insect predation on other insects. Schoenly (1990) also found that Hymenoptera accounted for the highest number of prey links (about 44%).

Memmott and Godfray (this volume Chapter 9) discuss parasitoid webs in further detail, and give examples of the complexity of some of these interactions. Attributes of the parasitoid lifestyle allow for greater complexity in food webs than other lifestyles because of the stability of interactions (see below).

Regulatory effect

An indication of the level of regulation that natural enemies exert in natural systems is the way in which phytophagous insects can display massive increases in population size when they are introduced into areas where their natural enemies are absent. In the cases of biological control discussed above, pests were not present in large population sizes in their native homes, which indicate that they are naturally held under some level of control.

Theoretical models have been produced which show that parasitoids are potentially able to regulate hosts at lower population density than would exist in their absence (Hassell, 1986; May and Hassell, 1988; Huffaker and Gutierrez, 1990a,b). However, the best evidence that parasitoids can regulate population size of phytophagous insects comes from biological control. There are numerous instances of reduction in the population size of an introduced phytophagous insect after the introduction of native parasitoids (DeBach and Rosen, 1991; see above). The impact of natural enemies in successful biological control programmes can be evaluated by excluding them, either through pesticide use or mechanical exclusion, to see how the pest population reacts in their absence (DeBach *et al.*, 1976; Huffaker and Gutierrez, 1990b, DeBach and Rosen, 1991).

DeBach and Rosen (1991:8) illustrated a California lemon tree nearing

complete defoliation. The natural enemies had been destroyed by repeated applications of DDT, and the resulting increase in the population of the California red scale (*Aonidiella aurantii*) was close to killing the tree. A nearby lemon tree, not treated with DDT and shown for comparison, was healthy and had dense foliage. The DDT spray released the scale from the regulatory effect of its two parasitoids, *Aphytis melinus* and *A. lingnanensis* (Aphelinidae), which normally hold the scale under complete or substantial control through most parts of California. DeBach and Rosen (1991) list several other examples of pest resurgences caused by chemical misuse, many of which involve parasitic Hymenoptera. Each of these examples is an illustration of a parasitoid regulating a host population at a level far below that at which the host would occur in the absence of parasitoid.

Further indication that parasitoids, and in particular parasitic Hymenoptera, do regulate herbivore populations outside of agroecosystems comes from numerous examples of naturally occurring biological control (Hagen *et al.*, 1971; MacPhee and MacLellan, 1971; Rabb, 1971). DeBach and Rosen (1991) listed 23 documented cases of natural biological control. In many of the examples cited in these works, phytophagous insects which are known to have the potential to occasionally produce heavy damage are maintained at a low population level due to the presence of a natural enemy complex. The occasional pest outbreaks are usually the result of some disruption of the natural enemy complex.

Examples of keystone parasitic Hymenoptera

Solbrig (1991:52) discussed that class of keystone species which contained, 'keystone predators, herbivores, parasites, and pathogens that allow the maintenance of diversity among competing organisms by reducing the abundance of the dominant competitors and preventing competitive exclusion'. Clearly many parasitic Hymenoptera belong to this category; parasitoids help to maintain diversity in other species by regulating the population of herbivores that would otherwise out-compete, and thus eliminate, other herbivores. The clearest examples of this again come from biological control.

Species of parasitic Hymenoptera used in successful biological control programmes are keystone parasitoids. They have a direct effect by lowering the population size of their host, and can have a variety of indirect effects. A simple example of an indirect effect would be if the removal of a keystone parasitoid allowed a herbivore population to expand to the point where it out-competed, and thus eliminated, other species of herbivores. In a more extreme example, the herbivore population would increase to the point where it eliminated its plant host.

Laing and Hamai (1976) listed about 150 different species of parasitic Hymenoptera which were supplying some level of control (partial, substantial, or complete) in biological control programmes. This list represents 150 species which have been seen to have a measurable effect on the population size of their host, and thus 150 documented examples of keystone species in the parasitic

Hymenoptera. Few groups can rival this number of documented keystone species, and these are only the documented cases. Equally important are the thousands upon thousands of undocumented cases of naturally occurring biological control involving keystone species of parasitic Hymenoptera.

Rarity in Parasitic Hymenoptera

Rarity is of special interest in parasitic Hymenoptera. There is evidence that many parasitic Hymenoptera are naturally present in low numbers. Stork (1988:325), based on a study involving canopy fogging, stated, 'Ants dominate the Bornean samples with 4489 individuals but only 99 species. In contrast, 1455 Chalcidoidea are represented by 739 species, 437 of which were singletons with only 8 species having more than ten individuals – the commonest species having 19 individuals.' Stork's data show that although there are three times as many individual ants as chalcidoids, there are over seven times as many species of chalcidoids. In natural situations, parasitic Hymenoptera are often present in high species numbers and low population size.

This does not mean that these species of parasitic Hymenoptera are unimportant, indeed the rare species could be the most important. High population size is not necessarily a requisite of keystone species (Reid and Miller, 1989; LaSalle and Gauld, 1992). Because parasitic Hymenoptera can operate in a density-dependent manner, an effective parasitoid may maintain its host in low numbers, and therefore be in low numbers itself. It has been seen on many occasions that species of parasitoids which appear rare are very important in terms of regulatory effects. In examples taken from biological control studies (see above), keystone parasitoids are present in low numbers once they have established initial regulation of the pest.

Parasitoids which are rare in natural ecosystems may even be potentially the most useful as biological control agents. Myers *et al.* (1989) listed reasons why parasitoids might be rare in their native habitats. Many of these reasons were detrimental to their potential as biological control agents; however, others could contribute to a parasitoid's potential. Indeed, Myers *et al.* (1989) felt that species which are rare in native habitats may have the greatest potential as biological control agents for the following reasons:

1. Parasitoids which attack the less common late stages of their host might be less numerous, but they would have a greater effect on host dynamics because of lower density-dependent mortality in the later stages.
2. Parasitoids that are heavily attacked by hyperparasitoids or predators might only persist through high fecundity, thus they may have potential for rapid increase when introduced into an area free of their own enemies.
3. Hosts might not have developed resistance to parasitoids which are rare in the native habitat.

Although it might be beneficial that parasitic Hymenoptera can maintain host populations, and thus their own populations in small numbers, and that parasitic Hymenoptera which are rare in their native habitat might make the best biological control agents, rarity makes a species more sensitive to environmental perturbations. The ability of parasitic Hymenoptera to regulate their hosts at low populations, and thus be in low numbers themselves, may make them more susceptible to extinctions or local extirpations (see below).

Extinction and Parasitic Hymenoptera

Extinction in relation to Hymenoptera has been discussed by LaSalle and Gauld (this volume Chapter 1). This section treats special factors of the parasitoid life-style which make parasitic Hymenoptera extinction prone, and offers examples that parasitic Hymenoptera are more sensitive to environmental disturbances than their phytophagous hosts. This means that parasitic Hymenoptera will suffer extirpation or extinction before their hosts, and thus release those hosts from any regulatory effect.

When parasitoids effectively regulate their hosts at a low population density, this endangers them by making them a species with a chronically small population, as well as meaning they are dependent on an unreliable resource. In any given herbivore–parasitoid relationship, the minimal population size necessary to avoid local extirpation (or extinction) will be higher in a species of parasitic Hymenoptera than its host. This is due not only to genetic constraints peculiar to the Hymenoptera (see Unruh and Messing, this volume Chapter 2), but also to resource availability. Herbivorous insects do not have as complex searching requirements as parasitoids, which, upon finding the proper host plant, still have to locate a suitable host species in a specific stage.

Localized extirpations of parasitoids due to population fluctuations are not uncommon, and these can result in small, isolated pest outbreaks in areas under general biological control. Such outbreaks are short lived, because they are readily colonized by parasitoids from surrounding areas. However, increasing habitat fragmentation may result in such outbreaks where there is no longer an accessible pool of parasitoids to colonize the expanding host population.

There is a variety of direct evidence which shows that parasitic Hymenoptera are more susceptible to environmental disturbances. Disturbances which eliminate populations of parasitic Hymenoptera or disrupt their activity can be detected by (often dramatic) increases in their host populations. Examples of such environmental disturbances include pesticide use and the presence of man-made or naturally occurring dust.

1. *Pesticide use.* This is the best documented evidence that parasitic Hymenoptera are more extinction prone than their phytophagous hosts, and there are a multitude of examples of pest upsets caused through the application of chemicals.

References are too numerous to list, however for examples and representative references see van den Bosch (1978), and the following sections in DeBach and Rosen (1991): Fostering pests through the misuse of pesticides; Upsets of natural balance by chemicals; Insecticides: the ecological narcotics. As mentioned above, a standard method for the evaluation of biological control involves using high dosages of pesticides which will extirpate parasitoids, and thus allow the pest populations to increase unchecked. This procedure consistently produces the same result: the same level of environmental disturbance will eliminate parasitic Hymenoptera, but does not eliminate their phytophagous hosts.

2. *Dust*. Dust has long been known to have an adverse effect on parasitic Hymenoptera (Bartlett, 1951). The presence of dust 'interferes with the action of parasites and kills parasites as effectively as many pesticides' (Rose and DeBach, 1990:419), and pest outbreaks in areas under biological control are often found next to dirt roads, where traffic produces dust. Naturally occurring dust, such as volcanic ash, can also affect parasitic Hymenoptera. Hashimoto *et al.* (1987) noted a reduced rate of parasitization of the arrowhead scale, *Unaspis yanoensis*, during periods of greater than normal volcanic activity, presumably due to the adverse effects of the ash on its aphelinid parasitoids.

Genetic diversity

The same factors which cause extirpations and extinctions will also cause a decline in the genetic diversity within a population or a species. Not only is high genetic diversity of potential benefit to biological control, it might also be important to the overall survival of a species facing rapidly changing environmental and habitat conditions (Unruh and Messing, this volume Chapter 2).

Parasitic Hymenoptera and the Maintenance of Biodiversity

Lessons from biological control

As stated previously, information gained from biological control studies can provide insights into other areas. Of particular interest is the possible effect of removal of keystone parasitoids.

The same basic pattern is regularly repeated in classical biological control: a species is not a pest in its native home (indeed it is often rare) due to regulation by its natural enemy complex; it is moved from its native home, thus releasing it from the regulatory effect; it achieves pest status in its introduced home; its natural enemies are found, introduced into its new home, and re-establish regulation. The keystone role of the pest's natural enemies is not known until they are removed.

This pattern may be similar to what we can expect if we release herbivores

from regulation through environmental perturbations. Removal of a keystone parasitoid, which will normally be deleted from the system before its host, can result in a marked increase in the host population. One important difference between this scenario and a biological control case: the environmental perturbations might ultimately cause species extinctions of natural enemies so that we have no means to acquire natural control measures for the new pests.

The ramifications of this extend beyond agricultural pests. Pests of tropical forest trees are likely to become more noticeable in the future when the focus of tropical forestry turns from harvesting to the development of sustainable silviculture. At that point, parasitic Hymenoptera, which have already played a major role in biological control projects against forest pests (see reviews by Turnock *et al.*, 1976; Waters *et al.*, 1976), will be indispensable. Unfortunately, the present rapid destruction of tropical hardwood forests (Erwin, 1988; Myers, 1988) may also be destroying the organisms necessary to preserve much of what remains of their diversity when the move to reforestation takes place.

Biological control has also shown us the value of genetic diversity within keystone species (see Unruh and Messing, this volume Chapter 2). The same factors which cause local extirpations and extinctions will also cause loss in genetic diversity, and thus perhaps the loss of the ability of a species to be a successful regulatory agent under certain environmental conditions.

Finally, biological control has provided some of the best evidence that parasitic Hymenoptera are an extinction prone group, and an indication of the cascade effect if keystone species of parasitic Hymenoptera are lost.

Cascade effect from removal of keystone parasitoids

Tests for evaluating impact of natural enemies in biological control programmes require the removal of the (keystone) species which are providing the control (DeBach *et al.*, 1976; Huffaker and Gutierrez, 1990b), thus allowing us to actually observe cascade effect.

In the example showing the regulatory effect of parasitic Hymenoptera given above, two species of parasitic Hymenoptera were excluded from a citrus tree under biological control (DeBach and Rosen, 1991). The removal of these two species resulted in such a massive population explosion of California red scale, that it could have caused the defoliation, and ultimate death, of the citrus tree. Such an action can influence a multitude of other species. Bennett *et al.* (1976) listed ten phytophagous Homoptera alone associated with citrus in California; there are also a variety of other phytophagous insects and mites associated with citrus, and a complex of natural enemies associated with each herbivore. A citrus tree could conceivably be the home of several hundred species of arthropods, all of which could be destroyed by the removal of only two species of parasitic Hymenoptera.

The idea of a single pest species destroying all of the citrus trees in California might seem far fetched, however it has come very close to happening. In the mid-

1880s the cottony cushion scale (*Icerya purchasi*), which was rare in its native Australia, had devastated the California citrus industry to the point of destruction. The biological control success through the importation of its natural enemies (in this case a beetle and a fly) was so spectacular that it saved citrus in California and established biological control as a viable means of pest management (see Doutt, 1958; DeBach and Rosen, 1991).

Using this as an example, it is possible to envision local extirpations occurring where plant species, and thus their specific herbivores, are sparsely represented in fragmented habitats. The chance loss of one or two species of parasitic Hymenoptera could result in an increase in the population size of a herbivore. This might not always result in the extirpation of the plant species, but could easily result in extirpations of several less competitive species of herbivore. When a large proportion of the world's biodiversity is confined to fragmented habitats (as may soon be the case), local extirpations may well be equal to extinctions. If these extinctions contain keystone species, then one extinction can lead to others.

An additional consequence of the removal of a keystone parasitoid might be the added reliance on pesticide usage. Current agricultural practices will not allow a pest insect to go unchecked; if natural enemies cannot be found to control it then pesticides will be used. Increased pesticide usage will surely contribute to the ecological problems the planet is already facing (van den Bosch, 1978).

Parasitic Hymenoptera and ecosystem stability

Parasitoids contribute greater stability to ecosystems than other lifestyles, and, as stated before, slightly over 75% of insect parasitoids are Hymenoptera (Eggleton and Belshaw, 1992). Toft (1986:455) pointed out that '... on a time scale exceeding one generation, characteristics of the parasitoid lifestyle enhance both the ability of parasitoids to regulate the lower trophic level and the stability of the interaction compared to predators'. Pimm and Lawton (1978) found that more levels in food chains were possible with parasitoid interactions than other lifestyles due to a greater stability of these interactions.

Parasitoids with specialized behaviour may confer even greater stability than other parasitoids. Systems with heteronomous hyperparasitoids are more stable than systems with regular hyperparasitoids, and deviant male ontogenies in parasitoids may serve to add greater stability at both the population and community levels (Hassell *et al.*, 1983; see above).

Thus, merely by their lifestyle, parasitic Hymenoptera help to maintain ecological balance by providing greater stability to the ecosystems in which they occur. Since there is a multitude of species which occur in virtually all terrestrial ecosystems, this represents a substantial beneficial effect on the planet.

Conclusions

Previous sections have shown that parasitic Hymenoptera play a vital role in community balance; that their removal might result directly in increases in population size of hosts, and indirectly in the loss of herbivore or even plant species; and that they are an extinction prone group of organisms. The importance of parasitic Hymenoptera to biological control has been established, and implications for conservation biology which can be found in biological control projects have been discussed. Biological control has provided many documented examples of keystone species of parasitic Hymenoptera, as well as indications as to the type of cascade effect which might be expected from the loss of parasitic Hymenoptera species in natural ecosystems.

We cannot predict the effect of the loss or decline of a large number of parasitic Hymenoptera species. It is obvious that not all species of parasitic Hymenoptera will be keystone species. It is equally clear that generalist species will not be as susceptible to extinction as their specialist relatives. What is important is that we have no way of predicting which species are keystone species before they are removed. Changing agricultural and forestry practices mean that we do not know which phytophagous species might become pests. If their parasitoids have already been removed, it will not only facilitate their achieving pest status but will deny future generations recourse to biological control.

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Parasitoid Webs

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Introduction

Studies of the diversity of animals in general, and of parasitoids in particular, typically begin with the analysis of the number of species and individuals in a community (Erwin, 1983; Stork, 1987; Noyes, 1989). Such data are valuable in the detection of patterns in diversity, but normally reveal only a limited amount about the ecological processes underlying these patterns. A richer source of information is provided by food webs which define the trophic relationships between the species and a community. Community ecologists have constructed food webs to understand energy flow through communities, and to understand the population and community dynamics of large assemblages of species (Cohen, 1978; Cohen *et al.*, 1990; Pimm, 1982; Pimm *et al.*, 1991). Rather few food webs include substantial numbers of parasitoids. In this chapter we argue that studies of food webs containing parasitoids are essential in interpreting patterns of parasitoid diversity, and are also useful in guiding research on the population dynamics of parasitoid assemblages. Ideally, parasitoids should be studied in combination with the competitors, predators and pathogens that also influence the distribution and abundance of their hosts. This will seldom be possible, but much information can be gained from what we call parasitoid webs: subsets of food webs that describe the linkage between hosts and parasitoids in a single habitat.

This chapter consists of four sections. First, we distinguish between a variety

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of types of parasitoid web, and describe their relationship to standard food webs. Second, we discuss some problems in parasitoid biology that can be addressed by parasitoid webs and, third, we review the parasitoid webs present in the literature. Finally, we discuss techniques and problems associated with the construction of parasitoid webs, illustrating the discussion with our own experience of building a parasitoid web around the leaf miners in a tropical dry forest in Costa Rica.

Food Webs and Parasitoid Webs

Three types of food web are normally distinguished: community webs, sink webs and source webs (Cohen, 1978). Community webs describe the relationships between all predators and prey (and ideally detritivores and saprovores) within a habitat or set of habitats. Source webs and sink webs are focused on a single species and include, respectively, all its predators and higher trophic levels, or all its prey and lower trophic levels. Community webs are obviously the most valuable of the three types of food web as they describe a whole community and are not biased by the choice of focal species.

Food webs are complex structures and there has been much research on the development of summary statistics that describe their salient features and allow comparison between food webs (Pimm, 1982; Cohen *et al.*, 1990). Important statistics used to describe food webs include the following:

1. The total number of species in the web, the numbers in the different trophic levels, and the numbers of levels.
2. Connectance: the number of actual trophic interactions divided by the number of possible interactions.
3. The average interaction strength between the species in the web.
4. The ratios of species in different trophic levels, for example the ratio of predators to prey.
5. The degree to which the web is divided into discrete compartments.
6. The presence and importance of species feeding at more than one trophic level.
7. The presence of cycles in the web: for example, instances where species A feeds on B which feeds on C which feeds on A.

Turning to parasitoids, data are occasionally collected on all the possible hosts of one species of parasitoid (as in a sink web) and very frequently on the parasitoids and hyperparasitoids of one species of host (as in a source web). In this chapter we shall have little to say about host source webs which have been extensively analysed over the last five years by Hawkins and his colleagues (Hawkins, 1988, 1990; see also this volume Chapter 10; Hawkins and Lawton, 1987; Hawkins and Gagné, 1989; Hawkins *et al.*, 1990). Indeed, it is some of the patterns revealed by this work that we see in need of explanation. Instead we

concentrate on parasitoid community webs which we define as a diagram linking all the hosts that are connected by shared parasitoids in one particular habitat, as well as any hyperparasitoids present in the system.

Parasitoid webs can be constructed in a number of different ways and we distinguish three main types:

1. Connectance webs which show which species of parasitoids attack which host, but with no quantitative information on the relative importance of different associations.
2. Semi-quantitative webs which describe the relative abundance of different parasitoid species attacking each host, but not the relative abundances of hosts in the environment.
3. Fully quantitative webs which show the abundances of both hosts and parasitoids so that the frequency of each interaction can be expressed in the same absolute units (per metre per day for example).

Webs also vary in the degree to which they include data collected at different times and in different places. A few (typically connectance) webs are restricted to a limited number of parasitoid taxa.

The Use of Parasitoid Webs

Parasitoid webs can be used for a variety of purposes. First, they can be used in the same way as traditional food webs. Properties such as connectance, compartmentalization and trophic ratios can be calculated and their values in different webs compared (Pimm and Lawton, 1980). When sufficient webs are available, it will be possible to search for properties that are conserved across webs, and to look for ecological correlates of more variable web features. It will also be possible to compare parasitoid webs with food webs dominated by other types of natural enemies. In addition to what might be called standard food web analysis, parasitoid webs can be used to address a variety of problems and hypotheses specifically related to parasitoid biology.

Parasitoid species load

Studies of the parasitoid assemblages attacking individual host plants have led to the detection of a number of different patterns in parasitoid species load. For example, there is a clear relationship between parasitoid species load and host feeding niche: leaf-mining insects tend to have the greatest number of parasitoids with fewer found on species feeding in more exposed sites (leaf folds, spinings and external feeders), and also fewer found on endophagous herbivores feeding in more concealed sites (galls, stems, roots) (Hawkins and Lawton, 1987; Hawkins, 1988). Hawkins has proposed that this pattern can be explained by differences in the ease with which parasitoids locate hosts in different feeding niches, and the degree to which the hosts are protected from predation. A

second, and less clear pattern, is for greater parasitoid species loads to be found on herbivores of trees and shrubs in comparison with herbivores on low-growing plants (Hawkins *et al.*, 1990). A possible explanation for this pattern is that parasitoids find greater difficulty locating hosts on early successional plants dispersed throughout the habitat.

To fully understand and explain patterns of parasitoid species load, it is necessary to know the degree to which hosts share parasitoids. Recruitment of a specialist to a host's parasitoid tally must involve evolutionary change while recruitment of a polyphagous species might purely involve ecological processes (or even sampling effects). It is not normally possible to assess host specificity from parasitoid load data which concentrate on a particular host species. This is because there may be further hosts in the same habitat which are not sampled. Some progress can be made by equating the degree of host specificity with the koinobiont/idiobiont dichotomy (Askew and Shaw, 1986; Sheehan and Hawkins, 1991). An idiobiont parasitoid kills or permanently parasitizes its host at the time of attack while the host of a koinobiont recovers and resumes feeding, only later being killed by the parasitoid larva.

Koinobioncy and idiobioncy are taxonomically conserved traits so the biology of unknown species can be inferred from knowledge of the biology of related species. However, at best such methods will be approximate and data from parasitoid webs are required to assess the comparative importance of specialists and generalists in determining parasitoid species load.

In discussing differences in parasitoid species load on early and late successional plant species, Hawkins *et al.* (1990) considered the influence of herbivore radiations. Leaf-mining moths in the genus *Phyllonorycter* feeding on trees have a greater parasitoid species load than those feeding on herbs, possibly because there are very few species on the latter class of plants compared with the large radiation on trees and shrubs (Askew, 1975, 1980; Askew and Shaw, 1986). In contrast to *Phyllonorycter*, dipterous leaf miners in the family Agromyzidae are very much more diverse on herbs than trees, and their parasitoid species load appears to be highest on early successional plants. Without parasitoid web data it is difficult to assess the importance of herbivore radiations on the pattern of parasitoid species loads.

Tropical and temperate parasitoid diversity

There has been much discussion about the relative diversity of temperate and tropical parasitoid communities since Owen and Owen (1974) argued that the diversity of tropical Ichneumonidae in Africa was less than or equal to the diversity of the same taxon in the British Isles. This was a surprising claim because most groups of herbivorous insects are more diverse in the tropics and there had been a tacit assumption that parasitoid diversity mirrored that of their hosts. The argument today revolves around two issues: is the pattern true, and if so, what causes it?

The Owens' results, which were based on samples of parasitoids collected in malaise traps, were confirmed by Janzen and Pond (1975) using sweep net sampling. However, Hespeneide (1979), Morrison *et al.* (1979) and more recently Noyes (1989) have pointed out that sweep nets tend to collect large insects in exposed situations and are a poor way to collect very small species. It is possible that parasitoid diversity increases in the tropics although the number of species of particular taxa, such as the Ichneumonidae, shows a reverse trend (as happens in a number of herbivore groups such as the Agromyzidae).

If the pattern is true, how might it be explained? Janzen and Pond (1975; also Janzen, 1981) proposed the resource fragmentation hypothesis: phytophagous insect populations are so widely dispersed among the diverse tropical flora that individual host species are too rare to support specialist parasitoids. Generalist parasitoids should be less affected by resource fragmentation since they do not depend on a single host population. Alternatively, Rathcke and Price (1976) have suggested that predation pressure on parasitoids may be higher in the tropics and preferentially afflict parasitized hosts. They suggest that parasitoids are partially excluded by predators. Yet another suggested explanation is that communities in a stable, tropical environment are dominated by competition and reduced diversity results from competitive exclusion among parasitoids.

The analysis of parasitoid webs will help resolve a number of these contentious issues. First, comparison of webs based on similar guilds of herbivores (for example leaf miners or external folivores) will provide primary data on the diversity of parasitoids independent of sampling technique. Whereas sweep netting and insecticide fogging may select for particular types of parasitoids, rearing is relatively unbiased. Thus parasitoid webs can help establish whether there is something that needs explanation. Second, parasitoid webs will help distinguish the competing hypotheses. The resource fragmentation hypothesis makes concrete predictions about the relative frequency of host-parasitoid associations that can be tested with fully quantitative parasitoid webs. The different hypotheses make different predictions about the distribution of specialist and generalist parasitoids in tropical and temperate regions. Although the koinobiont/idiobiont dichotomy can be used as a surrogate measure of host specialization (Hawkins *et al.*, 1992), it is a very coarse tool in comparison with actual data from parasitoid webs. Finally, some parasitoid webs may show patterns in community organization that reveal the structuring force of competition. For example, competition is suggested if most herbivores have exactly one specialist parasitoid, while a random (Poisson) or aggregated distribution of specialists across hosts is suggestive of a less structured community.

Apparent competition

Two host species that never directly interact can still influence each other's abundances if they share the same parasitoid species. If one species increases in abundance, the shared parasitoid will also be able to increase in density and the

second species will suffer elevated parasitism. Thus the population growth rate of each species suffers when the other becomes more common, exactly as happens in true competition. Holt (1977) described the parallel process mediated through parasitoids and natural enemies as apparent competition.

Parasitoid webs help in understanding apparent competition in two ways. First, by quantitatively describing the extent to which hosts share common parasitoids, they reveal the potential for indirect interactions via natural enemies. Second, they may reveal evidence for the patterns predicted by apparent competition theory (Holt, 1977; Jeffries and Lawton, 1984). For example, hosts may evolve temporal niche separation as a means of avoiding the effects of shared parasitoids (Gilbert and Singer, 1975). Apparent competition may also influence the host insects' choice of food plant. For example, enemy free space has been suggested as confining rare *Heliconius* species to a restricted range of larval host plants. This allows the larvae to escape attack from parasitoids afflicting the more common *Heliconius* species (Gilbert, 1984). Parasitoid webs can of course only provide indirect evidence for the importance and presence of apparent competition. To obtain direct evidence it is necessary to conduct manipulative experiments and to observe the effect of changes in the density of one host on the density of other species.

Keystone species

The population dynamic theory of host-parasitoid interactions is sophisticated and highly developed (Hassell and Pacala, 1990). Parasitoids are tractable animals for population dynamic experiments, and their importance in biological control has also spurred interest in their dynamics. Much of the theory has concerned single, specialist parasitoids attacking one species of host, although some studies have considered several specialists attacking one host (May and Hassell, 1981), one parasitoid attacking several hosts (Holt, 1977, and see above) and the interaction between specialist and generalist parasitoids (Hassell and May, 1986). In reality, outside artificial agroecosystems, such simple host-parasitoid systems are probably rare. However, this does not necessarily mean that most host-parasitoid theory is over-simple.

Although there may be a complex web of interactions linking many hosts and parasitoids, one or a few interactions may numerically dominate the system. We can informally illustrate this point by describing a parasitoid web on which we have partial data. In wet meadows at Silwood Park in southern England, between 10 and 20 agromyzid flies can be found mining the leaves of herbs and grasses. The flies are attacked by between 30 and 40 parasitoids, chiefly Eulophidae, Pteromalidae and Braconidae (all Hymenoptera). About half the species are specialists, attacking one or a few species of fly, while the other half have wider host ranges and include a few species that attack non-dipteran leaf miners. A connectance web would depict the system as a cat's cradle of shared interactions, suggesting that a description of the population dynamics of the system

Table 9.1. Summary of the properties of major parasitoid webs.

System	Feeding niche	Number of species	Quantification	Temperate /tropical	Spatial summation	Temporal summation
Oak galls	Gall wasp	61(62)	Semi-quantified	Temperate	Yes	Yes
Leaf miners on trees	Leaf miner	24(32)	Semi-quantified	Temperate	No	No
Aphids on trees	Sap sucker	21(38)	Connectance	Temperate	Yes	Yes
Gall midges on <i>Atriplex</i>	Gall fly	26(51)	Semi-quantified	Temperate	No	No
Gall midges on coyote brush	Gall fly	7(8)	Semi-quantified	Temperate	No	No
Weevils on dock	Stem miner	8(24)	Connectance	Temperate	Yes	Yes
Mistletoe herbivores	Mixture of herbivores	3(23)	Connectance	Temperate	Yes	No
Dry forest leaf miners	Leaf miners	86(220)	Fully quantified	Tropical	No	No

Feeding niche: the feeding niche of the parasitoid host insect.

Number of species: number of hosts and parasitoids in web, total number of organisms in web shown in parentheses.

Level of quantification: Connectance, semi-quantified or fully quantified.

Temperate or tropical webs: whether the web is constructed in the tropical or the temperate zone.

Spatial summation: if the web has been constructed from data collected from several sites.

Temporal summation: if the web has been constructed from data collected over several field seasons.

would be extremely complex. However, a fully quantitative parasitoid web would reveal that one species, the common buttercup miner *Phytomyza ranunculi*, numerically dominates the host trophic level, exceeding the abundance of other species probably by an order of magnitude. Its dynamics are most likely dominated by a few species that concentrate on this host, although it also supports many rarer generalist species. It is interesting that generalists that constitute a small fraction of the parasitoid species attacking this very common species of host may be in absolute terms very common and have an enormous impact on the dynamics of other species. Thus the dynamics of *Phytomyza ranunculi* may be little affected by the other hosts in the community while the dynamics of these hosts are largely driven by changes in the abundance of the common species.

The idea that communities may be dominated by a few 'keystone' species has a long pedigree in community ecology (Paine, 1966; Pianka, 1978). Their presence in parasitoid communities will considerably increase the ease with which our understanding of simple host-parasitoid systems extends to the study of more complex communities. Parasitoid webs can never prove the dynamic importance of keystone interactions as they are snapshots of static populations and so are very limited in what they tell us about dynamics. Yet fully quantitative webs give strong indications about the relative importance of different interactions and provide strong suggestions about likely keystone species.

Community Parasitoid Webs

We are aware of no fully quantitative, community parasitoid webs, as defined above, that encompass more than a few hosts. However, there is a variety of connectance and semi-quantitative webs that provide important insights in parasitoid community structure. In this section we review the main features of a number of these webs and how they have been constructed. Table 9.1 summarizes some of their properties and also includes a new web that we describe in the next section.

Oak galls

The web describes the interactions between gall wasps (Hymenoptera: Cynipidae), inquilines and parasitoids (Askew, 1961). The data are principally, although not entirely, from a single location, an area of woodland in southern England. The rearing records are summed over a three-year period. The web is large, describing a parasitoid complex of 61 species. The web is presented as a series of source webs, describing the interactions of each gall wasp species. The web is semi-quantitative although the relative number of different gall species collected provides an approximate indication of host abundance.

One feature of this web is the large amount of facultative hyperparasitism.

Many species of parasitoids will attack the host plus any other parasitoid already feeding on the host. Facultative hyperparasitism is best regarded as an interaction occurring within a trophic level. The alternative, viewing each occurrence of one species feeding on another as adding a new trophic level, can be misleading. Schoenly *et al.* (1991) recently treated the oak cynipid web as containing eight trophic levels and yet it is very unlikely that any particular gall is hyperparasitized more than once or twice.

Food webs which are divided into compartments are believed to show greater dynamic stability than non-compartmentalized webs (May, 1972, 1973). A compartment is a group of species which interact strongly among themselves, but only weakly with other members of the community. Pimm and Lawton (1980) used statistical methods to test whether Askew's food web contained greater compartmentalization than would be expected by chance. They concluded that there was no evidence for compartmentalization although they stressed their study should be regarded as preliminary. It would be interesting to know whether functional compartments would be detected if quantitative rather than connectance data were employed in the analysis, and also whether the oak-cynipid web is itself a compartment within a larger woodland food web.

The web clearly shows that gall form and position have a major influence on the parasitoids attacking the cynipid gall maker. Askew (1980) has suggested that the avoidance of parasitoid attack may be the chief evolutionary factor influencing the diversity of gall forms. The parasitoid complement of each species is also influenced by gall phenology. A variety of different levels of host range can be distinguished among the different gall wasp parasitoids. A few species are strictly restricted to one host species while others attack all gall makers and parasitoids found within a single gall. Other species attack different gall formers belonging to the same genus.

Leaf miners on trees

Askew and Shaw (1974, 1979; Shaw and Askew, 1976) provided a detailed account of the parasitoids attacking the leaf miners of British deciduous trees. Data were collected over four years on all groups of leaf miners, although with an emphasis on gracillariid moths in the genus *Phyllonorycter*.

Most species of leaf miner are attacked by between ten and twenty species of parasitoid. Some parasitoids are very polyphagous, but the majority show some preference for particular groups of miners. The hosts belong to four orders of insect: Lepidoptera, Hymenoptera, Coleoptera and Diptera. Askew and Shaw (1974) showed that while the first three orders tended to have similar parasitoid faunas, the fauna of dipterous miners was rather different. At a lower level of resolution, host plant had a major influence on the parasitoids attacking different miner species. The genus *Achrysocharoides* (Eulophidae), for example, consists of *Phyllonorycter* specialists. In the majority of cases, each species is restricted to one species of host plant and attacks all *Phyllonorycter* species on that plant.

While gall morphology has a major effect on parasitoid communities, leaf miner structure is much less important, probably because miner structure is comparatively uniform. Askew (1980) suggested that the uniform morphology of miners and the presence of generalist parasitoids may prevent miners diversifying on one host plant to the same extent as the morphologically heterogeneous cynipids which share fewer common parasitoids. Askew and Shaw (1986) found evidence that the length of time the host spent on the mine was correlated with the number of parasitoid species by which it was attacked. Bivoltine species of miner were also subject to different levels of attack in different generations, indicating the influence of miner phenology. Obligate hyperparasitoids are rare or absent, though facultative hyperparasitism is common and widespread.

Aphids on trees

Rejmanek and Stry (1979) discussed 31 webs reconstructed from data in the literature on primary (but not secondary) parasitoids of aphids on different plants. They used the webs to examine the relationship between connectance and species richness. May (1972, 1973) had suggested that reduced connectance in larger webs may counteract the link between greater complexity and instability predicted by theoretical studies. Rejmanek and Stry (1979) indeed observed a decrease in connectance in larger webs, an example of the use of a parasitoid web to answer general questions from food web theory. The webs also show that the food plant is a major determinant of parasitoid host range.

Gall midges on *Atriplex*

The web describes the natural enemies attacking 12 species of gall midge (Diptera: Cecidomyiidae and Agromyzidae) found on two species of saltbushes (Chenopodiaceae: *Atriplex* spp.) in California (Hawkins and Goeden, 1984). In addition to primary gall formers, the web includes inquilines, predators, parasitoids and hyperparasitoids. Some of the more generalist parasitoids found in this community attack other hosts in the environment and a few are very polyphagous. There is evidence that the web is compartmentalized as groups of species that interact strongly among themselves but weakly with other groups can be identified. Generalist parasitoids attacking several host species play an important role in this system. Different species of gall maker are active at different times of year and host phenology has a strong influence on parasitoid faunas. In particular, galls available throughout the year were attacked by specialists while species with a more restricted season were only attacked by generalists. Gall morphology had only a minor effect on the composition of parasitoid faunas.

The importance of phenology in this community of parasitoids mirrors Askew's (1961) findings for the oak gall community. Washburn and Connell (1979, 1981) also argued that the seasonal transfer of parasitoids from one host

to another is important in American oak cynipid parasitoid communities. Hawkins and Goeden (1984) argued that the structure of the gall midge parasitoid community on *Atriplex* is strongly influenced by competitive interactions between parasitoids. The importance of competition among parasitoids is a hotly debated issue.

Gall midges on the creosote bush

The web describes the interactions between a single species of gall midge (*Rhopalomyia californica*) on coyote brush (Asteraceae: *Baccharis pilularis*), its parasitoids and hyperparasitoids (Force, 1974). Like Hawkins and Goeden (1984), Force (1974) believed that the parasitoid community was structured by competition and in a series of elegant laboratory experiments he demonstrated a variety of subtle interactions between different parasitoid species.

Weevils on dock

The web describes the parasitoid complex associated with a guild of stem boring weevils (*Apion* spp.) on dock (Polygonaceae: *Rumex*) (Hopkins, 1984). It was not possible in all cases to associate individual host and parasitoid species so the web is to some extent poorly resolved. Although some species are specialists on dock weevils, other species are probably more polyphagous.

Mistletoe herbivores

The web describes the community of herbivores and their natural enemies found on mistletoe (Whittaker, 1984). It was constructed to test Gilbert and Singer's (1975) suggestion that herbivores partition a shared host plant. The study provides a detailed description of the insect fauna of mistletoe at one site, including their natural enemies.

We have too few parasitoid webs to begin to make comparative statements about what properties are common to many webs or correlate with ecological variables. In particular, there are no fully quantitative food webs although several webs are semi-quantitative. The webs available are certainly not a random selection of parasitoid webs. All of the webs are centred around herbivorous insects, and the majority endophagous insects, in particular gall formers. Cecidomyiidae (gall midges) are particularly well presented. All the webs concern temperate parasitoid communities where the majority of parasitoid community ecologists live and work. Webs often contain data collected in different seasons or from different localities. Finally, and encouragingly, most parasitoid webs identify all taxa to species level. This is relatively unusual in food web studies and markedly increases the value of the data.

The Construction of a Quantitative Parasitoid Web

The specific aim of the Costa Rican leaf miner project was to construct a quantitative food web describing the interactions between plants, leaf miners and their parasitoids in an area of tropical dry forest. The web as a whole will be used to address a number of questions including:

1. Do strategies of resource utilization differ between temperate and tropical regions?
2. Can patterns in the number of parasitoid species attacking different herbivores, and the percentage mortality caused by parasitoids, be explained by biological characters of the host species?
3. To what extent is the structure of the parasitoid community influenced by host plant characteristics?
4. How important is seasonality in tropical parasitoid communities?

We believe that the best way of answering such questions is through the use of a quantified food web.

We chose leaf miners as model herbivores for three reasons: Firstly, leaf miners are relatively simple to sample quantitatively as their feeding tracks leave a semi-permanent record of their activity and their fate. Secondly, leaf miners suffer heavy parasitoid attack but their parasitoids are typically restricted to leaf miners. Thus, leaf miner parasitoids form a self-contained community. And thirdly, data exist on temperate leaf miner/parasitoid communities which can be used for comparing patterns of parasitoid community structure. The leaf miners were sampled throughout the rainy season as there were temporal changes, both quantitative and qualitative, in the leaf miner community in the plot. A shorter season would result in a web describing only a section of the parasitoid community.

The field site was in an area of tropical dry forest in the Guanacaste National Park, Costa Rica. The forest has a pronounced dry season lasting approximately six months. Leaf miners are extremely scarce during this period and they were sampled only during the wet season. The aim of the project was to study the complete guild in one small area rather than a few members of the guild over a large area. This study area was a plot (100 m by 190 m) of second growth forest. Only the understorey was sampled as it was difficult to sample the forest canopy at all, let alone quantitatively.

Sampling and rearing

The understorey leaf miners were sampled by running 100 m transects across the plot. Transect lines were placed at 10 m intervals and the order in which they were used was randomized. All leaf miners found within 1 m either side of the transect line and up to approximately 3 m in height were collected. Leaf miners were collected along transects at approximately ten-day intervals. Additional leaf

miners were collected from within the plot in order to increase the number of insects reared. Leaf miners were also collected from other areas of secondary forest in order to assess how representative the plot miner–parasitoid interactions were of the area in general.

Leaf miners were reared individually in plastic rearing pots or in small plastic bags. Methods best suited to individual species were developed throughout the field season. During the course of parasitoid web construction, approximately 5000 leaf miners were reared over two seven-month field seasons.

Taxonomy

Many of the insects reared were species new to science and new genera were discovered among the parasitoids. This was not a problem as the project was a collaborative venture between a taxonomic institute (The Natural History Museum) and an ecological institute (Imperial College at Silwood Park). Because of the taxonomic participation, all species of insect could be identified to morphotype. For the purposes of constructing a quantitative food web, identification to morphotype is sufficient.

Preliminary results

Two webs describing plant–leaf miner–parasitoid interactions were constructed for the plot, one for the 1989 and one for the 1990 field season. The web from the 1990 field season consists of 53 species of plant, 81 species of leaf miner and 86 species of parasitoid. The leaf miners were from three orders of insect: Coleoptera, Lepidoptera and Diptera. The complete web is extremely complicated. However, a great many of the leaf miners and parasitoids are extremely rare and the quantified web is considerably less complex.

As in Askew and Shaw's (1974) study, leaf miner host order influences parasitoid web structure. The web can be resolved into three sub-webs describing the three host orders. The Lepidoptera and Coleoptera webs share a number of parasitoids while the Diptera fauna is more distinct – exactly the same pattern found in the deciduous leaf miner guild. The coleopterian leaf miners are dominated by hispine beetles. The hispine parasitoid fauna is shown both as a connectance web (Fig. 9.1(a)) and as a fully quantified web (Fig. 9.1(b)). The four hispine species that feed on the three species of bamboo cannot be differentiated as young larvae and are grouped together in both webs. Recent work has shown that the lumping of the four species can be justified as the four species share many parasitoids (Mommott, pers. obs.).

The connectance web shows all of the interactions observed in the plot between plants, miners and parasitoids during the field season. The quantified web shows only those interactions observed during quantitative sampling. Rare interactions are thus excluded from the quantitative web. The absolute abundance of both leaf miners and parasitoids is shown as the number reared per

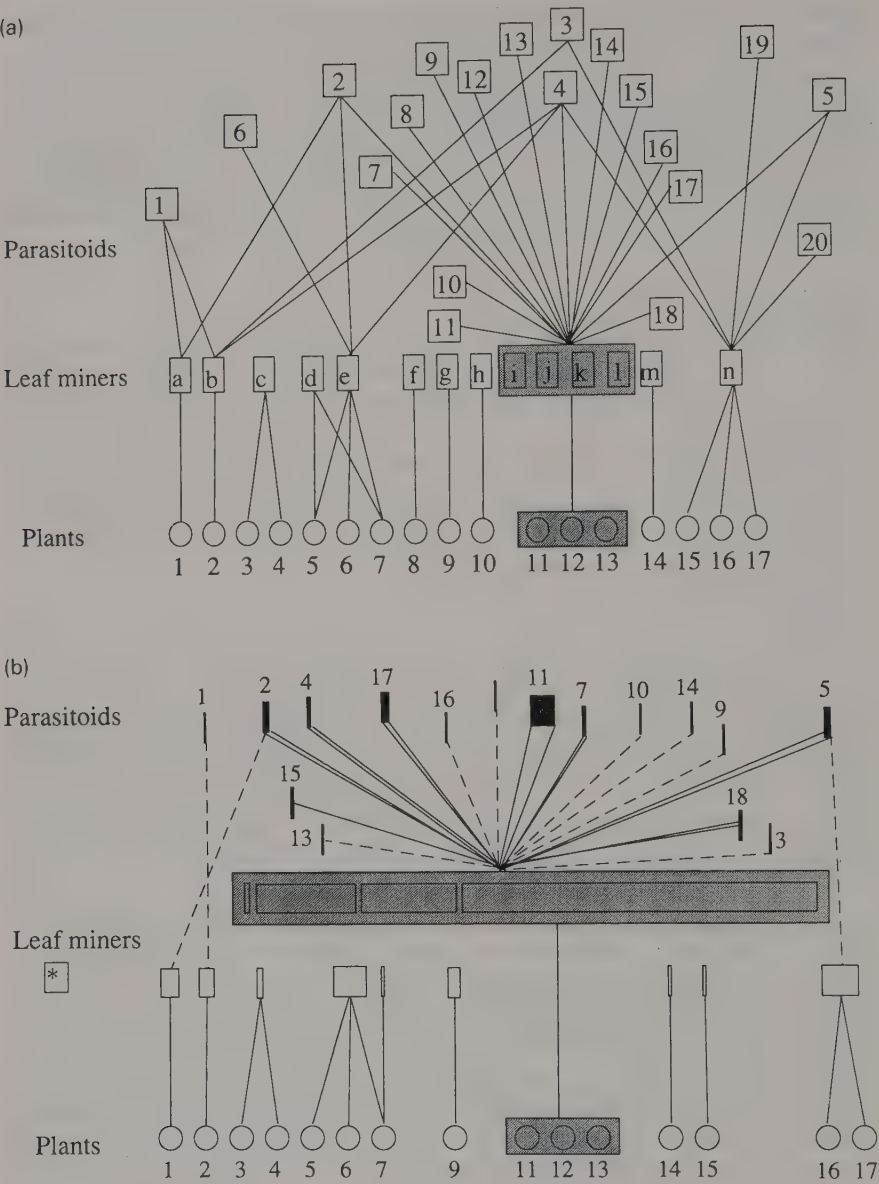


Fig. 9.1. The plant-hispine-parasitoid food web. (a) Connectance web displaying all of the interactions in the plot. (b) Quantified web showing the absolute abundance of leaf miners, parasitoids and interaction strength. The first rectangle (*) in the leaf miner level represents 30 miners-parasitoids reared per 1000 m².

Plants: (1) *Arrabidaea mollissima* (Bignoniaceae), (2) *Olyra latifolia* (Graminae), (3) *Compositae* sp.1, (4) *Compositae* sp.2, (5) *Centrosema pubescens* (Fabaceae), (6) *Dioclea megacarpa* (Fabaceae), (7) *Desmodium* sp. (Fabaceae), (8) *Cassia hayesiana* (Caesalpinaceae), (9) *Lantana camara* (Verbenaceae), (10) *Banisteriopsis* sp. (Malpighiaceae), (11) *Laciatis nigra* (Graminae), (12) *L. ruscifolia* (Graminae), (13) *L. procerrima* (Graminae), (14) *Sida* sp. (Malvaceae), (15) *Luehea* sp. (Tiliaceae), (16) *Helictes baruensis* (Sterculiaceae), (17) *Waltheria glomerata* (Sterculiaceae),

Leaf miners (Chrysomelidae:Hispinae): (a) *Uroplata fusca*, (b) *Heptispa* sp., (c) *Pentispa vittatipennis*, (d) *Sumitrosis roseus*, (e) *Oxychalepus auticornis*, (f) *O. postdatus*, (g) *Uroplata* sp., (h) *Sumitrosis* sp. (i) *Chalepus* sp.1, (j) *C. amabilis*, (k) *C. digressa*, (l) *C. horni*, (m) *Heterovispa virula*, (n) *Baliosus* sp.1.

Parasitoids: (1) *Bracon* sp.2 (Braconidae), (2) *Bracon* sp.1 (Braconidae), (3) *Conura* sp.5 (Chalcididae), (4) *Conura* sp.8 (Chalcididae), (5) *Chrysocharis* sp.1 (Eulophidae), (6) *Bracon* sp. (Braconidae), (7) *Conura* sp.2 (Chalcididae), (8) *Elasmus* sp.3 (Elasmidae), (9) *Conura* sp.6 (Chalcididae), (10) *Hemiptarsenus* sp.1 (Eulophidae), (11) *Conura* sp.1 (Chalcididae), (12) *Conura* sp.6 (Chalcididae), (13) *Conura* sp.7 (Chalcididae), (14) *Horismenus* sp.4 (Eulophidae), (15) *Conura* sp.10 (Chalcididae), (16) *Allobricon* sp.2 (Braconidae), (17) *Chrysocharis* sp.2 (Eulophidae), (18) *Chrysonotomyia* sp.2 (Eulophidae), (19) *Pnigalio* sp.1 (Eulophidae), (20) *Horismenus* sp.1 (Eulophidae).

1000². The absolute abundance of the plant species and the strength of the plant-miner interaction are also known although they are not shown in the figure.

The connectance web (Fig. 9.1(a)) shows a considerable difference in the parasitoid load of the 16 hispine beetles. This web gives no idea of how available each of the hispine species is to the parasitoids. The quantified web, however (Fig. 9.1(b)), shows the web to be dominated by a guild of four hispine species feeding on bamboos. Twelve species of parasitoid were reared from these hispines in the plot, but as can be seen from the quantified web, only a few have the potential to affect the hispine population. Only two polyphagous parasitoids are recorded in the quantified web and in each case they interact with the bamboo hispines more strongly than with the other host. The quantified web is a more accurate description of host-parasitoid interactions in the plot. It is also much simpler, with many weak and only a few strong interactions.

Conclusions

The construction of parasitoid webs is probably the greatest challenge in parasitoid community ecology. Until a representative sample of different webs is

available it seems unlikely that we shall make great progress in answering many of the outstanding problems of hymenopteran and parasitoid diversity. Although connectance and semi-quantitative webs are valuable, fully quantitative webs are much more powerful and repay the extra work involved in their manufacture. An interdisciplinary approach to this venture is probably essential: a good understanding of the natural history of hosts and parasitoids is a prerequisite for their successful rearing, and the skills of both ecologists and taxonomists are required in building the web. Ecologists need to be convinced that large assemblages of parasitoids can be identified while taxonomists need to be shown that quantification is worth the extra effort!

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Refuges, Host Population Dynamics and the Genesis of Parasitoid Diversity

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Introduction

There is little doubt that the parasitoids represent one of the most speciose and important ecological groups on the planet (LaSalle and Gauld, 1992; LaSalle, this volume Chapter 8). However, the actual number of species remains poorly known, and recent estimates of the number of species of parasitic Hymenoptera, the order containing the bulk of parasitoids, span one and a half orders of magnitude (LaSalle and Gauld, 1992). Thus, attempts to describe and understand geographic patterns of parasitoid diversity which depend on a detailed knowledge of the number of species in different parts of the world will remain greatly hampered until our taxonomic knowledge of the relevant groups is much improved. The same can be said of many of the insect groups which parasitoids utilize as hosts; with a few exceptions, global patterns of species diversity for the hosts of parasitoids also remain poorly documented, and given the scope of the task and the taxonomic resources available will likely remain so for some time to come.

This chapter draws together four alternative approaches to the study of parasitoid–host interactions which reduce (but by no means eliminate) the effects of incomplete taxonomic knowledge of parasitoids and their hosts. Using these four comparative techniques, I hope to accomplish two goals. First, I document quantitatively the species richness of parasitoid communities and their importance to the population dynamics of their hosts. Second, I propose that all of the resultant patterns of parasitoid–host interactions can be accounted for by a single, unifying factor. My hypothesis is basically that the extent that hosts occupy

refuges from parasitoid attack, largely provided by the plant parts on which they feed, drives the number of parasitoid species that can attack a host species and the susceptibility of hosts to parasitoid attack, and consequently the ability of parasitoids to impact their hosts' population dynamics.

The idea that refuges influence parasitoid–host interactions is not new. It has been widely suggested in the theoretical and empirical literature that refuges from natural enemies constrain both the number of parasitoid species that attack a host species (Shaw and Askew, 1979; Bauer, 1985; Askew and Shaw, 1986; Hawkins and Lawton, 1987; Price and Pschorn-Walcher, 1988) and the ability of parasitoids to regulate host populations (Beddington *et al.*, 1978; Hassell 1978; Price *et al.*, 1980; Murdoch *et al.*, 1985; Price and Clancy, 1986; Price, 1988; Luck, 1990). However, most workers have examined only one to a few parasitoid–host systems and have treated either host population regulation or parasitoid community richness separately (but see Gross, 1991). Here, examining hundreds to thousands of cases, I propose that refuges exert a major influence on many, perhaps most, parasitoid–host systems and that refuges provide a simple conceptual link for understanding both community level and population level processes simultaneously.

The first approach I use, rather than focusing on the total diversity of parasitoids and hosts which co-exist in an area, examines how parasitoid diversity is distributed among host species, i.e. patterns of variation in the species richness of parasitoid assemblages on individual host species. This represents a resource-based approach that links the studies of diversity and community structure. Further, analysing many individual parasitoid assemblages provides a basis for generating hypotheses about the constraints on the diversity of parasitoid communities and, by extension, global parasitoid diversity.

The second approach incorporates the results of the empirical study of species richness into a mathematical model. The scope of the problem precludes broadly based experimental tests of the hypotheses generated from comparisons of thousands of parasitoid–host systems. As an alternative, incorporating the constraints on parasitoid species richness identified by the empirical data explicitly into a model allows us to evaluate if it is even possible to generate the observed patterns. If it is possible to duplicate the patterns with an independently derived model, this represents an alternative method for evaluating the potential importance of the organizing forces operating in real parasitoid–host systems.

To fully understand parasitoid communities, it is important to document the dynamics of the interactions between parasitoids and hosts as well as their species richness patterns. Parasitoid–host associations are highly interactive with repercussions to both parasitoid communities and host populations. Parasitoids often represent a major source of mortality of their hosts, and parasitoids can be critical to the depression and regulation of host populations, as evidenced by the successful suppression of insect pests by parasitoids introduced for biological control (DeBach, 1974). Classical biological control introductions represent large-scale experiments which test the ability of parasitoids to impact host

populations, and numerous comparative analyses have been based on the outcomes of such biological control attempts (Hall and Ehler, 1979; Hall *et al.*, 1980; Greathead, 1986; Stiling, 1990; Waage, 1990; Gross, 1991). The third approach I use represents a similar analysis to examine the forces that influence the impact of parasitoids on hosts.

Finally, although the biological control record represents a valuable tool for examining parasitoid–host interactions, the generality of the results may be difficult to judge because both the parasitoids and hosts have been extracted from the more complex food webs in which they are naturally embedded. A comparative analysis of parasitoid-induced host mortality using native host–parasitoid systems thus represents an additional approach for evaluating the impact of parasitoids on hosts. I analyse here a data set using mortality levels of hosts studied within their natural ranges caused by native parasitoids which have not been intentionally manipulated.

Data and Methodology

Parasitoid community richness analyses

The species richness data represent an updated and expanded version of a global parasitoid data set compiled over the past six years (Hawkins and Lawton, 1987, 1988; Hawkins, 1988, 1990; Hawkins *et al.*, 1992), and consist of lists of parasitoid species recorded from individual host species from four orders of holometabolous herbivorous insects (Coleoptera, Diptera, Lepidoptera and Hymenoptera). Generally, lists were generated from primary literature sources only, except when a secondary source included references to primary sources which could be consulted to check the reliability of the records. In the analyses here, the parasitoid lists include primary and facultatively hyperparasitic parasitoids attacking host larvae and pupae only, although a few egg–larval parasitoids have undoubtedly been inadvertently included when they were partially identified and belong to genera which are not universally egg–larvals, and workers did not report that parasitoids reared from larvae actually attack eggs. Thus, known egg, egg–larval and adult parasitoids and obligatory hyperparasitoids were excluded. Finally, only hosts studied within their presumed native ranges were included.

Following previous methodology (Hawkins, 1990), separate parasitoid lists were generated by country for smaller countries and by state or province for larger countries (i.e. USA, Canada, Brazil, India and China). For the former USSR, separate lists were generated for each republic, except for Russia, where lists were generated by administrative region (Oblast). Thus, when a host species had been studied in several smaller countries, the country with the longest parasitoid list was used; when a host had been studied in several regions within a large country, the region with the most parasitoids was used. This methodology has

two effects. First, it minimizes the influence of differences in intensity of study in different countries, since the vast majority of hosts have been studied only once in a particular country or in the individual states/provinces/republics of North America, China, India or the USSR. Second, it reduces species-area effects by decreasing the areas over which a host has been studied in large countries to within the range of areas in which hosts have been studied in smaller countries.

Using the above criteria, the data set includes the parasitoids of 2188 host species in 110 families, studied in 86 countries in all major biogeographic regions of the world. Of the 12079 parasitoid records, 87.2% represent Hymenoptera, 12.5% represent parasitic Diptera and 0.3% represent other orders or are unidentified.

The foundation of the analysis of parasitoid species richness is the feeding biology of hosts. Eight types of hosts are distinguished: (i) external folivores; (ii) leaf rollers/webbers/tiers; (iii) casebearers; (iv) leaf/needle miners; (v) gallers; (vi) borers of stems, flowers, or fruits; (vii) root feeders; and (viii) mixed exophytic/endophytic feeders (i.e. herbivores which switch between exophytic and endophytic feeding during larval development or which are exposed when moving from one endophytic feeding site to another).

Earlier analyses have suggested that host feeding biology represents the single most important influence on parasitoid assemblage size, and that the causal mechanism is the extent that plant parts on which herbivores feed provide protection against parasitoid attack through structural refuges (Hawkins and Lawton, 1987; Hawkins and Gagnè, 1989; Hawkins, 1988, 1990). The rankings of the first seven feeding biologies above are hypothesized to represent increasing refuges. For example, externally feeding folivores, being fully exposed, occupy no structural refuges, whereas rollers have a slight refuge within their shelters, but remain susceptible to parasitoids searching for exophytic hosts and often leave their shelters for varying lengths of time to feed or construct new ones. Casebearers, although also more or less exophytic, gain some additional protection by being fully encased. Among endophytically feeding hosts, leaf miners receive some protection by virtue of developing entirely within plant tissues, but otherwise receive little physical protection from mines; gallers are better protected but provide visual cues to their presence (their galls); and borers are both physically protected by surrounding plant tissues and generally well concealed. Root feeders occupy the most extensive refuge by being underground. This ranking based solely on structural refuges is undoubtedly overly simplistic and does not incorporate other types of potential refuges from parasitism. But it does provide a simple conceptual basis for interpreting the empirical patterns. The mixed feeding category, by definition, includes herbivores that occupy more than one refuge or which leave their refuge during larval development, and therefore cannot be ranked in relation to the other feeding biologies. The herbivores in the mixed category share some characteristics with leaf rollers, but are distinguished primarily because they feed endophytically at some point during the larval stage.

Parasitoid community richness model

Host feeding biology is hypothesized to reflect primarily the influence of structural refuges. However, it is impossible to quantify the extent that plant parts provide protection from parasitoids for each and every herbivore species, so the link between herbivore feeding biology and refuges cannot be directly tested. Further, the scope of the problem precludes experimental tests of the proposed link for more than a few herbivores (see Gross and Price, 1988, for example). Hochberg and Hawkins (1992) have taken an alternative approach, the goal of which was to examine explicitly the influence of structural refuges on parasitoid assemblage size using a mathematical model, and then to compare patterns of species richness predicted by the model with those found for the empirical data which use host feeding-biology as a ranked proxy variable for refuges. A match between predicted patterns (which reflect refuges) and empirical patterns (which reflect feeding biology) would provide independent evidence that the empirical patterns are driven by the strength of refuges occupied by hosts.

The model, which has been published elsewhere (Hochberg and Hawkins, 1992) is based on previous host-parasitoid models (Hassell, 1978; Hassell and May, 1986; Pacala *et al.*, 1990) and considers a single host population which has discrete and non-overlapping generations. Each generation, a proportion of the host population is vulnerable to parasitism by a range of specialist and generalist parasitoid species (initially 50 species of each) which have a hierarchical competitive ability within multiply parasitized host individuals (initially assumed to alternate between individual species of the two types of parasitoids).

The difference equations for the number of hosts, specialist parasitoids and generalist parasitoids in the next generation incorporate parameters describing the finite rate of increase of the host population, the proportion of the host population inaccessible to parasitism, and the proportion of hosts surviving intraspecific competition (assumed to be compensatory and incorporating the environmental carrying capacity of the host).

Parasitoids are given functional responses (relating parasitoid density to the average probability of a host escaping parasitism) which incorporate the searching efficiency of the parasitoids and the maximum number of hosts that each parasitoid species may attack in any given generation. Further, generalists are given numerical responses (the number of parasitoids attacking the host population) assuming that each species has alternative host species present.

The model examines two sources of variability in the vulnerability of hosts to parasitism. The first, spatial heterogeneity, has the effect of decreasing parasitoid searching efficiency with increasing parasitoid density, and is incorporated (assuming a negative binomial distribution) into the parasitoid functional responses. The second, structural refuges, represents partial or complete protection from attack when hosts develop in inaccessible locations, such as, for example, when hosts feed in galls, tree trunks or roots. It is modelled by assuming that in any given host generation, a certain proportion of the host

population is not attacked, irrespective of parasitoid density.

Basic assumptions of the model include:

1. non-parasitoid induced density-dependent mortality occurs after parasitism, and parasitized and non-parasitized hosts suffer equally;
2. all sex ratios are 1:1;
3. parasitoids do not search for hosts within the refuge;
4. the distributions of parasitism among all parasitoid species are independent of one another;
5. the number of generalist parasitoids of any given species attacking hosts is proportional to host density.

The model was analysed for set levels of host invulnerability with numerical simulations of 100 generations each (by which time the results had stabilized). The initial densities of all specialist parasitoids were set equal to one, and host density was set at the environmental carrying capacity. A parasitoid species was considered to be present in the parasitoid community if at least one adult was produced in the hundredth generation.

Parasitoid impact analysis

A potential relationship between host refuges and the ability of parasitoids to impact their host's populations has recently been examined based on the outcome of parasitoid introductions for the biological control of insect pests (Hawkins and Gross, 1992). The data were derived from the BIOCAT biological control database (Greathead, 1986; Waage, 1990), which contains over 4000 records of natural enemy introductions throughout the world. For each introduction of a larval or pupal parasitoid for the control of a holometabolous pest, the feeding niche of the host and the outcome of the introduction (unknown, parasitoid failed to establish, parasitoid established but no control observed, or some degree of control achieved) was recorded. Using the 1377 introductions for which outcomes are known, the pooled proportion of introductions against all hosts in each feeding class in which at least some degree of control was achieved and the pooled proportion of establishments resulting in some control were calculated.

The hypothesis being tested in this analysis was that refuges from parasitism, here again measured by host feeding biology, produce two effects, one on the species richness of parasitoids and the other on the impact of parasitoids on host populations. If refuges are important, well protected host species should be attacked by fewer parasitoid species than less well protected hosts and should not be as strongly limited by natural enemies. Thus, a positive relationship between the richness of the parasitoid community and the extent that parasitoids limit their hosts would be expected.

Hawkins and Gross (1992) compared the biological control data against the species richness of parasitoid assemblages on North American herbivores and

against an earlier version of the global species richness data which included egg and adult parasitoids and hyperparasitoids, and which did not include any hosts from continental Europe and north Asia. Here I re-examine the relationship using the more extensive global species richness data set. Further, I test for a predicted relationship (Hawkins and Gross, 1992) between biological control success rates and host mortality.

As Waage (1990) has pointed out, catalogues of biological control projects are highly imperfect records of the outcomes of parasitoid introductions on host populations. Probably the most severe potential problem is evaluating how meaningful a recorded 'success' really is. Our approach has been simply to treat all levels of success, i.e. partial, substantial and complete, as equal evidence that parasitoids have had some measurable impact on host densities, without attempting to quantify how severe the impact might have been.

Percentage parasitism analysis

To examine the susceptibility of native hosts to parasitoid attack, a percentage parasitism data set was generated with the sources also used to generate the parasitoid species richness data. Percentage apparent parasitism was recorded whenever workers provided data. Whenever studies encompassed several host populations or were done over several host generations, the maximum mortality level was used. Similarly, when multiple studies were available for an individual host species, the study reporting the highest percentage parasitism was used (which was not always the same study used to generate the species richness data). Finally, whenever possible only percentage parasitism of larval stages was used. However, in hosts which support mostly or exclusively larval-pupal parasitoids (e.g. many tephritids), or which pupate in the same location where larvae feed, mortality estimates from pupal collections were included. Under these criteria, mortality estimates were obtained for 819 host species in 80 host families from 73 countries.

It should be borne in mind that the accurate measurement of host mortality due to natural enemies is a non-trivial exercise (Van Driesche, 1983; Van Driesche *et al.*, 1991), and relatively few of the papers consulted to generate the mortality data used the detailed techniques required. Therefore, the parasitism data are subject to a large, but unquantifiable amount of measurement error. The absolute levels of mortality for different types of hosts are at best crude estimates, but as long as the data contain no strong systematic biases the information which they yield on relative differences in parasitoid-induced mortality should be suitable for comparisons with the other data sets.

The Patterns

Parasitoid community richness

In all previous analyses which have examined the mean number of parasitoid species per host species in relation to host feeding biology, the relationship has taken a dome-shaped relationship; leaf miners support the most parasitoid species, and both exophytics and better protected endophytics support fewer parasitoids. Incorporating continental Europe and northern Asia into the data does not alter that relationship (Fig. 10.1). The addition of casebearers, not distinguished in earlier analyses, indicates that they support on average similar numbers of parasitoid species as leaf miners. This is not entirely unexpected because 12 of the casebearers are actually casebearing leaf miners, *Coleophora* species (Lepidoptera: Coleophoridae); thus there are biological similarities for many of the hosts in the casebearing and leaf mining categories. Herbivores in the mixed exophytic/endophytic category support moderately rich parasitoid complexes, but because these hosts represent a grab bag of species with varied and often complex biologies and cannot be ranked in terms of the refuges they occupy, it is difficult to judge why they support the numbers of parasitoids that they do.

The factor hypothesized to account for the pattern of parasitoid species richness across the feeding categories is the extent that hosts occupy structural

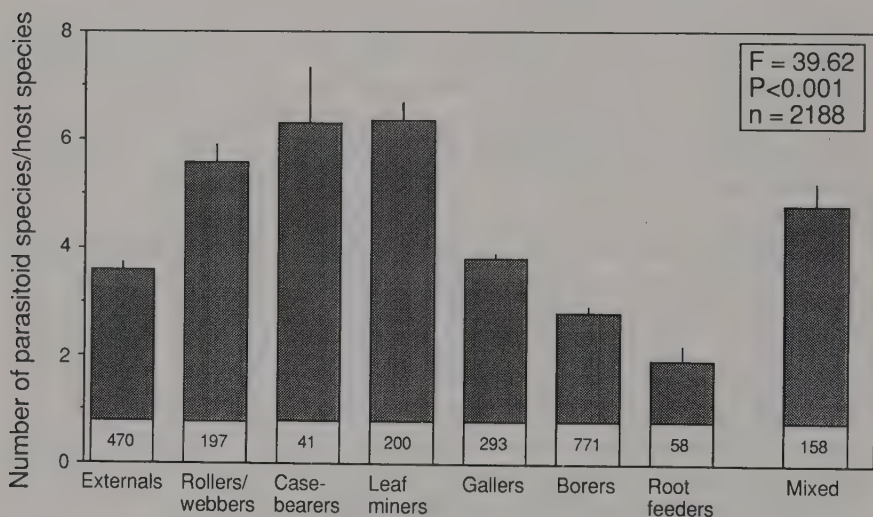


Fig. 10.1. The mean number (+ 1 SE) of parasitoid species per host species for eight categories of herbivores, based on how and where they feed as larvae. Means are back-transformed from analysis of variance of log-transformed parasitoid species richness. F -statistic from single-classification ANOVA. Numbers at bases of bars are the number of host species in each feeding category.

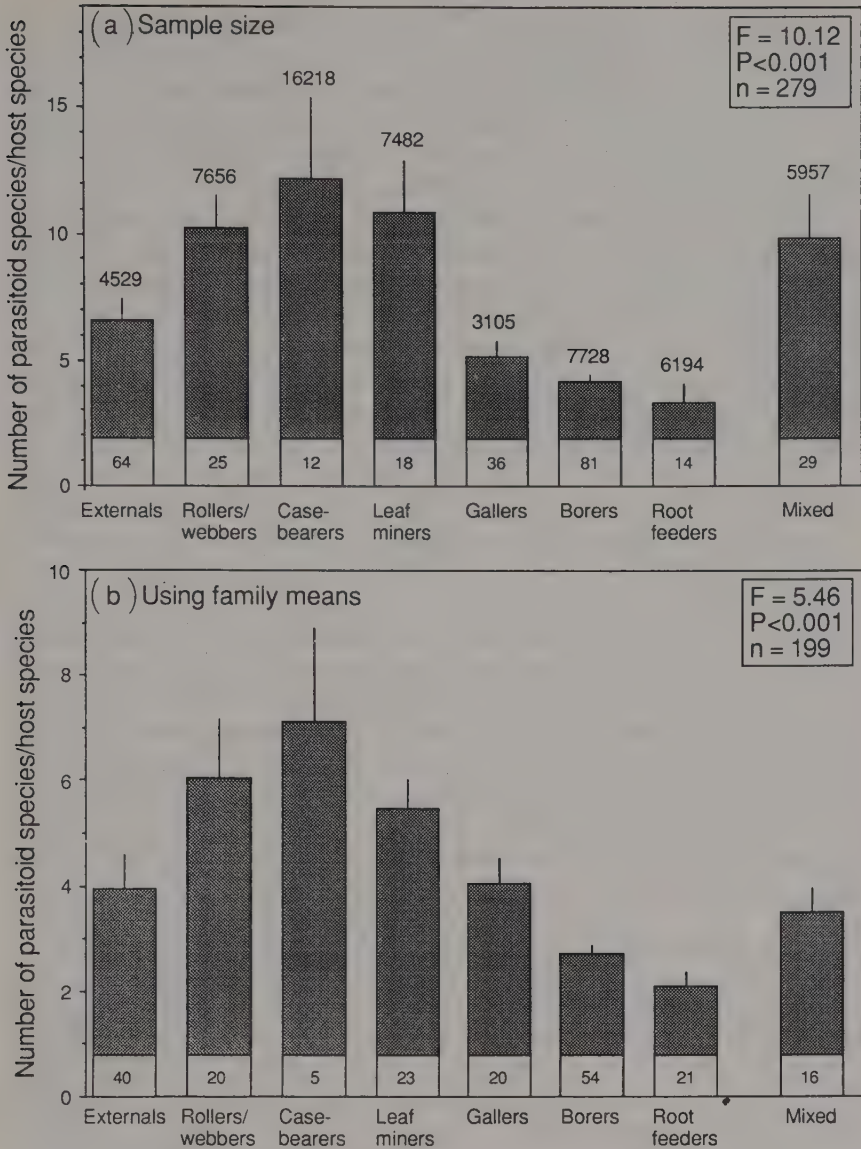


Fig. 10.2. Relationships between the number of parasitoid species per host species by herbivore feeding biology accounting for two possible confounding variables. (a) Sample size; including only hosts for which at least 1000 individuals were reared. Presentation as in Fig. 10.1, but the number above each bar represents the geometric mean sample size for hosts in each feeding category. (b) Weighted by host family; using mean parasitoid species richness for each host family in each feeding category. Hence, the numbers at bases of bars represent the number of host families used to generate each category mean.

refuges. If true, the interpretation of the pattern is that hosts which occupy a refuge of low to moderate strength support the most parasitoid species, and species in both smaller and greater refuges support fewer parasitoids. It is highly counter-intuitive that hosts occupying a very small structural refuge should support fewer parasitoids than hosts in a moderate refuge. That this is even possible will be examined in the next section.

Of importance here is determining that the relationship between parasitoid species richness and host feeding biology is not confounded with other factors which could explain the pattern, and determining the relative importance of host feeding biology in relation to other forces known to influence parasitoid species richness. There are at least two factors which could be confounded with feeding biology in this analysis: sample size and taxonomic heterogeneity among hosts. The first could be important if herbivores in some feeding categories are easier to sample than those in other feeding categories. This is undoubtedly true. For example, it must be easier to sample large numbers of individuals of a leaf miner species than of a root feeder. Therefore, it is possible that the different numbers of parasitoids from hosts in each feeding category reflect only that the parasitoid complexes of some hosts are better studied than others, and that this is associated with feeding biology.

The effect of sample size was initially examined by recording the numbers of hosts reared by the original workers. I then examined the relationship using only those hosts of which at least 1000 individuals were collected, assuming that a sample size at least this large should provide a reasonably complete picture of a parasitoid complex. Basing the analysis on 279 well-studied host species indicates that although parasitoid assemblages on hosts in all feeding categories are richer than indicated by the entire data set, the dome-shaped relationship is unchanged (Fig. 10.2(a)). This suggests that sample size does not by itself account for the differences among the feeding categories.

Table 10.1. Relative importance of five independent variables for explaining variation in the number of parasitoid species per host species (log-transformed) for 390 host species. *F*-statistics and the proportion of variance explained by each variable (R^2) considered individually were obtained from either single-classification analysis of variance (for feeding biology, plant type, mean low temperature and habitat) or linear regression (sample size, log-transformed). Variables are ranked in decreasing order of importance.

Variable	<i>F</i>	Probability	R^2
Host feeding biology	11.25	<0.001	0.171
Log sample size	68.44	<0.001	0.150
Host foodplant type	6.08	<0.001	0.045
Mean low temperature	2.90	0.022	0.029
Habitat	1.40	0.248	0.007

A potential bias could also arise due to non-independence among the data within each feeding category, arising from including multiple cases of closely related host taxa when they all feed similarly (Harvey and Pagel, 1991). For example, if most root feeders were scarabaeid beetles, and scarabaeids never support many parasitoids irrespective of where they feed, the mean parasitoid species richness for root feeders could be biased by the repeated inclusion of related species in that category. To examine the effect of including multiple cases of related host taxa within individual feeding categories, I calculated the mean number of parasitoid species per host species for all hosts in each host family in each feeding category. Thus, each host family is represented by a single value in each feeding class. This approach results in slightly richer parasitoid complexes than found when all host species are included individually, but the shape of the relationship with feeding biology is essentially unchanged (Fig. 10.2(b)). Thus, the association of parasitoid species richness and host feeding biology appears quite robust.

Host feeding biology clearly seems important to parasitoid species richness, but just how important is it? In the initial analysis of the parasitoids of 285 British herbivores, Hawkins and Lawton (1987) used multiple regression to rank the importance of seven ecological and biological characteristics of hosts to parasitoid species richness, and found that feeding biology accounted for an order of magnitude more variance in parasitoid species richness than did any other variable (20.5%, with a total explained variance of 22.1%). A re-analysis of the British hosts with the more refined data set used here (excluding homopteran hosts and egg or adult parasitoids and hyperparasitoids, giving 176 host species) results in an explained variance of 38.2%, with feeding biology explaining 25.1%, the geographical extent that hosts have been studied explaining an additional 9.1%, and herbivore foodplant type explaining 4.1% more. Thus, host feeding biology represents the most important correlate of parasitoid species richness in Britain, at least for the variables I am able to measure.

To rank the determinants of parasitoid species richness on a global scale, I have analysed five variables:

1. host feeding biology;
2. sample size;
3. herbivore foodplant type (monocot, herb, shrub or tree);
4. the mean temperature in the coldest month for the locality where the hosts were studied (Hawkins, 1990);
5. whether hosts were studied in natural or cultivated habitats (as in Hawkins *et al.*, 1992).

The analysis used 390 host species for which complete data were available. Linear regression and single-classification analysis of variance (ANOVA) indicate that feeding biology accounts for more variance than any other variable considered separately, including sample size, and that the remaining three variables account for little of the variance in parasitoid species richness (Table 10.1). An

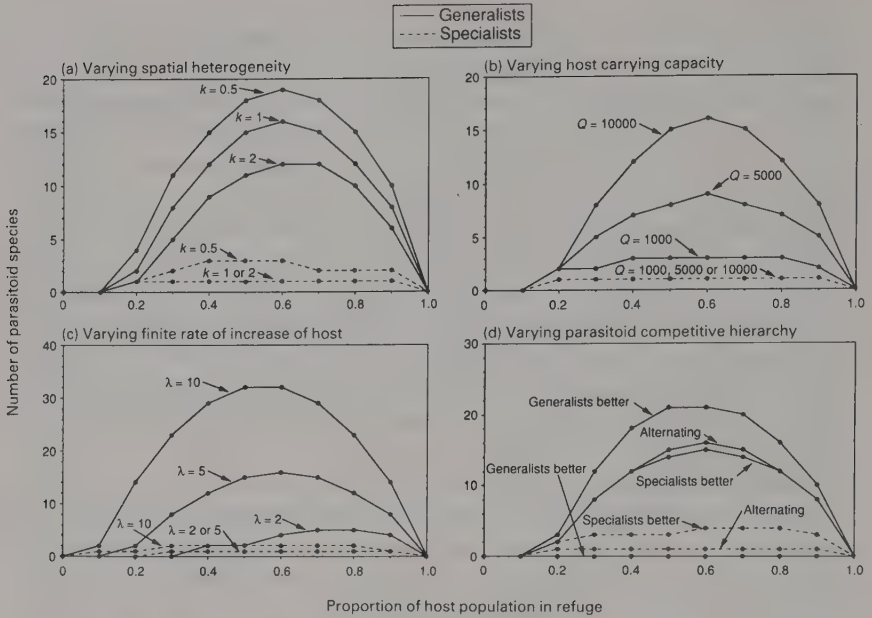


Fig. 10.3. Patterns of specialist and generalist parasitoid species richness across a refuge gradient generated by species richness model for different values of four model parameters. (a) Spatial heterogeneity; smaller values of k represent increasing heterogeneity in parasitoid search. Increasing heterogeneity increases parasitoid species richness. (b) Environmental carrying capacity (Q); more abundant hosts support more parasitoid species. (c) Host finite rate of increase (λ); increasing host fecundity increases the number of co-existing parasitoid species and shifts maximum species richness to smaller levels of refuge. (d) Varying within-host competitive ability in favour of one type of parasitoid (specialists or generalists) increases the species richness of that type at the expense of the other. (Note that the basic relationship between parasitoid species richness and refuge level is dome-shaped throughout these ranges of parameter values.)

analysis of covariance testing the effect of feeding biology with sample size as a covariate indicates that both are highly significant ($P < 0.001$), with host biology explaining 17.2% of the variance and sample size 15.1%. A preliminary test of the feeding biology \times sample size interaction was not significant ($P = 0.171$). Thus, both feeding biology and sample size contribute significantly to parasitoid species richness, but the former provides a slightly better predictor, and feeding biology and sample size influence parasitoid species richness independently.

Based on the available evidence, I conclude that how and where a host feeds represents the single most important determinant of parasitoid species richness. The next question is, does this pattern actually represent the influence of structural refuges?

The community richness model

In virtually all simulations, the patterns of parasitoid species richness across a gradient of increasing structural refuges results in a dome-shaped relationship (Fig. 10.3). Varying the values of other parameters and assumptions of the model modifies the actual levels of species richness at each refuge level, but the basic shape of the relationship is always retained; hosts in a moderate refuge support more parasitoid species than hosts in either very small or very large refuges.

The explanation for the basic pattern generated by the model is that when there is no physical refuge from parasitism, parasitoids drive the host population to very low levels, which reduces the number of parasitoid species which can persist in the community. As the proportion of hosts in a refuge increases, parasitoids are no longer able to drive host populations to such low levels, and more parasitoid species can maintain their own populations. However, there comes a point at which the proportion (and number) of hosts available for parasitism outside of the refuge begins to decrease to levels which force down parasitoid population levels, resulting in fewer parasitoid species able to persist. Ultimately, when all hosts are in the refuge, there are no susceptible hosts, and hence, no parasitoids.

There are two important points regarding the model, and a caveat. First, it is intriguing that it is possible to generate a community-level phenomenon (species richness) using a relatively simple model based on population dynamics, with refuges as the driving mechanism. Second, the qualitative pattern of variation in species richness predicted by the model is in very close correspondence with the empirical patterns based on host feeding biology. Moreover, for a reasonably wide range of parameter values, the quantitative levels of species richness agree with those found in most real parasitoid communities, which vary from 1 to 81 in the global data set. Thus, the hypothesis that a biological characteristic of hosts, how and where they feed, can account for the range of parasitoid diversities found in nature seems reasonable.

On the other hand, it is important to note that the model predicts no parasitoids when hosts do not occupy a refuge, but real exophytic hosts support on average 4–7 parasitoid species (Figs 10.1 and 10.2). This undoubtedly reflects that the real world is more complicated than the model or hypothesis indicates. It is clear that types of refuges other than the structural ones considered here exist in nature (Price *et al.*, 1980). For example, mobile external feeders may benefit from a probabilistic refuge by being able to move away from leaf damage to which parasitoids may orient (Hawkins and Gross, 1992). Even among sessile exophytics, refuges may arise through complex interactions among the particular plant part the host occupies, the sizes of susceptible host stages, and parasitoid searching efficiencies (Walde *et al.*, 1989), or hosts may occupy partial refuges provided by negative effects of ingested foodplant secondary chemicals on parasitoid development (Flanders, 1942). Other types of herbivores may similarly occupy additional types of refuges. It is likely that all herbivores occupy some

sort of refuge, even if it is small; otherwise they would be driven to extinction by natural enemies! When other types of refuges are incorporated into the model and hypothesis, at the very least the total proportion of hosts occupying their refuges will be shifted towards higher levels than indicated by structural refuges alone. It is also possible that when all types of refuges are considered, physical, chemical and behavioural, the overall ranking of hosts along the refuge gradient may differ in some cases from a ranking based on physical refuges only; we might, for example, expect leaf miners to be most susceptible to parasitoids since they are both poorly protected by plant tissues and can use only restricted behavioural escape mechanisms to avoid parasitism. Finally, this modelling effort is still in its infancy. Additional work is needed before we can be certain that the proposed mechanism, structural refuges, can fully explain the predictions of the model. Incorporating an additional variable into the model which takes into account the ability of herbivores which do not inhabit a structural refuge to escape from parasitoids through behavioural and chemical defences may better represent reality. But, despite these complicating factors, it is encouraging that large differences in parasitoid community size can be predicted using a simple model, and that the concordance of the model and the empirical data is generally quite good.

Parasitoid species richness and host population limitation

Is the number of parasitoid species that different types of herbivores support related to the impact that those parasitoids have on host populations? A regression of the mean number of parasitoid species per host species for herbivores in each feeding class (from Fig. 10.1) against the pooled proportion of introductions against similar kinds of pests which have resulted in some control (from Table 10.2) is significant and positive (Fig. 10.4(a)). To test that this result does not simply reflect that it is more difficult to establish parasitoids on hosts in some feeding types than on others, the regression was repeated only for those parasitoids which were successfully established. The relationship was significant (Fig. 10.4(b)). Thus, susceptibility to attack by greater numbers of parasitoid species is related to the ability of those parasitoids which do attack a host to depress host density.

This pattern is consistent with the hypothesis that refuges influence the ability of herbivores to escape from parasitoids in both evolutionary and ecological time. Because, for example, leaf miners are highly discoverable, they accumulate many parasitoid species. Further, most individuals in a population are susceptible to attack at some point during larval development, increasing the probability of density-dependent responses by parasitoids to changes in host density. Root feeders, on the other hand, occupy an extensive refuge which limits the number of parasitoid species which will ever encounter them, and which makes it more difficult for those parasitoids that can attack them to respond to changes in herbivore density. Thus, refuges link long-term colonization by parasi-

Table 10.2. The numbers of parasitoid introductions directed against holometabolous pest insects in six feeding categories with their outcomes.

Host type	Introductions	Failures ¹	Establishments ²	Control ³
Externals	293	189	66	38
Leaf rollers/tiers	41	28	8	5
Mixed	196	136	36	24
Leaf miners	89	52	21	16
Concealed	610	436	121	53
Root feeders	148	119	19	10
Total	1377	960	271	146

Source: From Hawkins and Gross (1992).

¹Failures = parasitoid not established.

²Establishments = parasitoid established but no control observed.

³Control = parasitoid established and some degree of control achieved.

roids and the short-term effects of parasitoids on host populations.

It is an important component of the pattern that external folivores are intermediate in both parasitoid species richness levels and the outcomes of parasitoid introductions on density depression (Fig. 10.4), even though they occupy no structural refuge. This probably reflects the effects of other types of refuges (host mobility, host foodplant chemistry, etc.) on susceptibility to parasitoid attack. It is relatively easy to rank endophytic hosts on a refuge gradient using structural refuges, but incorporating other types of refuges to quantify the overall susceptibility of exophytic herbivores to parasitoid attack is difficult, requiring a more detailed knowledge of herbivore biologies. Disentangling the effects of the multitude of forces that undoubtedly influence the parasitoids of exophytic herbivores remains a major challenge for understanding the full range of parasitoid–host interactions (Hawkins, 1990, Hawkins *et al.*, 1992). Nevertheless, refuges appear to offer broad explanatory power, even for exophytics, as long as we remain aware that ‘refuges’ can have numerous components.

A critical assumption underlying the interpretation of this analysis is that the rates of success of biological control attempts against herbivores depend on different levels of susceptibility to parasitoid attack by virtue of the strength of the refuges that hosts occupy. However, the connection is based on levels of parasitoid species richness rather than on direct measures of susceptibility. It logically follows that if the refuge hypothesis is correct, parasitoid-induced mortality levels on different types of herbivores in their native environment should also be related to biocontrol success rates in their adopted environment (Hawkins and Gross 1992), since it is the proportion of the host population susceptible to parasitoids that is believed to influence both host population limitation and parasitoid species richness. Using the averages of maximum parasitism

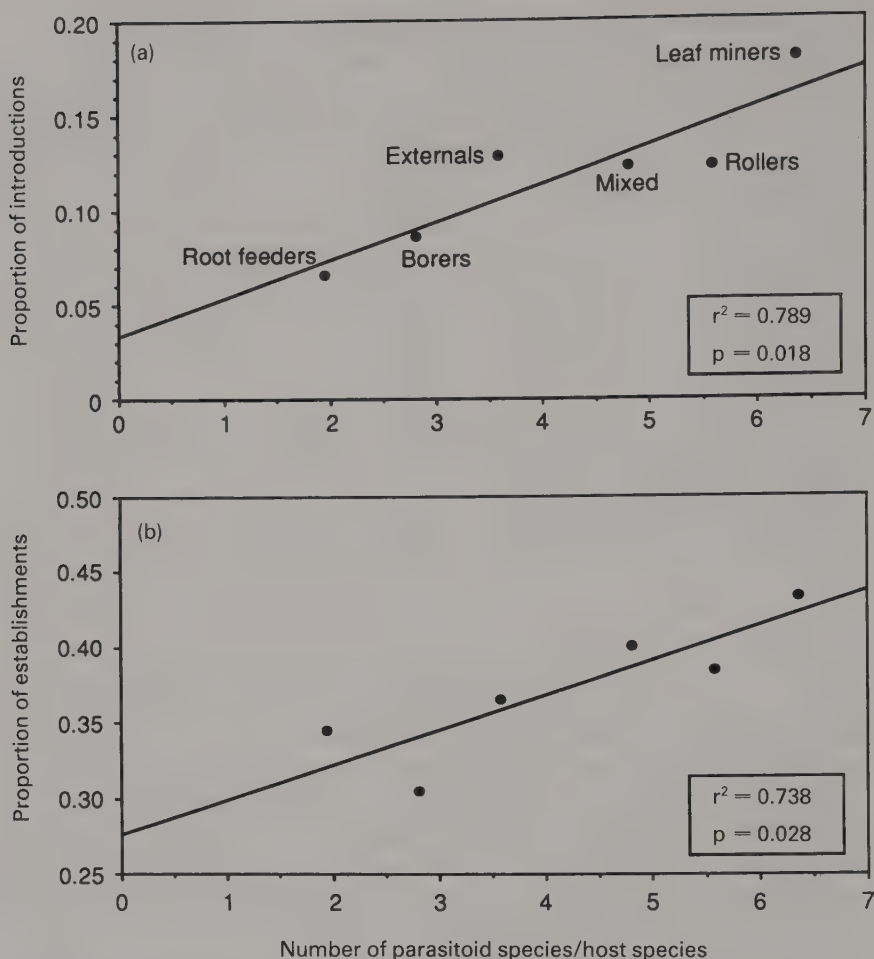


Fig. 10.4. Relationship between the mean number of parasitoid species per host species taken from global parasitoid data set and the outcomes of parasitoid introductions for the biological control of six types of insect pests. (a) The pooled proportion of introductions resulting in some level of control. (b) The pooled proportion of parasitoid establishments which have resulted in control of pest. Statistics from linear regression.

rates of native herbivore species generated from the global literature, the proportion of introductions which have resulted in some degree of control is strongly related to natural mortality levels for native host species (Fig. 10.5(a)). Correcting for differences in establishment rates among the different kinds of herbivores produces a result which just misses the 5% level of significance (Fig. 10.5(b)). This pattern provides additional, albeit imperfect, evidence for the influence of refuges on parasitoid–host interactions.

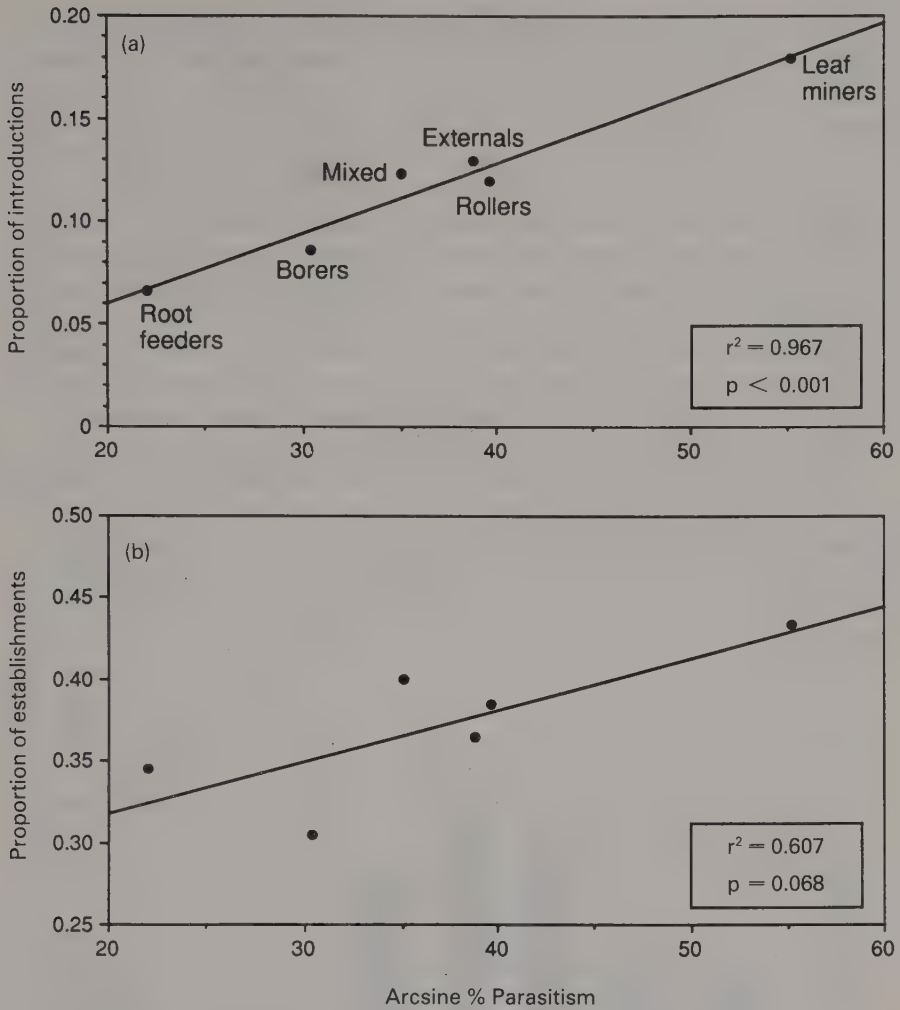


Fig. 10.5. Relationships between mean host mortality (see Fig. 10.6) and the outcomes of biological control attempts. (a) The pooled proportion of parasitoid introductions resulting in some level of control. (b) The pooled proportion of parasitoid establishments resulting in control.

Mortality levels in native parasitoid–host systems

The above analyses indicate a linkage between parasitoid species richness and the susceptibility of herbivore populations to parasitoid attack. However, targets for biological control by no means support ‘natural’ parasitoid assemblages, because most of the parasitoid species normally associated with the host species are absent in the introduced region. Introduced herbivores are often colonized by

parasitoids native to the area of introduction, but most of these new associations represent generalist parasitoids which attack the novel host at very low levels (Cornell and Hawkins, in prep.). Finally, the constellation of co-occurring herbivores which may act as reservoirs for a herbivore's parasitoids differs between native and introduced regions. Do these differences between the parasitoids associated with a herbivore in its native and non-native ranges fundamentally change the relationship between parasitoid species richness and susceptibility to attack?

Comparing rates of host mortality across herbivore feeding biologies for native herbivores results in a dome-shaped relationship very similar to that for parasitoid species richness (Fig. 10.6). Thus, feeding biology broadly influences host mortality in much the same way as it does parasitoid species richness. Ignoring host feeding biology by directly comparing mortality and species richness for each host species results in a highly significant, but noisy, positive correlation ($F = 85.30$, $df = 817$, $P < 0.001$, $r = 0.307$). The relatively low explained variance ($= 9.5\%$) is not unexpected given that both variables contain errors, with the mortality estimates being especially error prone. Nevertheless, this analysis suggests that parasitoid species richness and host mortality are coupled in native parasitoid–host communities. This relationship seems to reflect the effects of differences in susceptibility to parasitoid attack, partly explained by host feeding

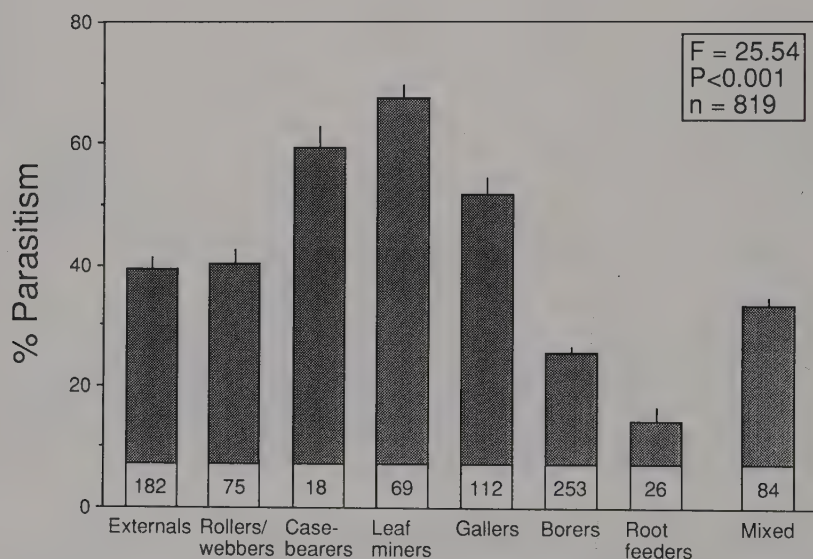


Fig. 10.6 Mean parasitoid-induced mortality levels (± 1 SE) of native herbivores in eight feeding categories. Means are back-transformed from analysis of variance of angular-transformed maximum reported parasitism rates. F -statistic from single-classification ANOVA. Numbers at bases of bars represent the number of host species in each feeding category.

biology, and these effects are maintained when hosts and parasitoids are transferred to non-native locations.

Conclusions

Parasitoid–host systems represent species rich communities, in which large numbers of parasitoid species often co-exist on individual host species. Further, parasitoids are frequently responsible for substantial levels of mortality of their herbivorous hosts. As regards the Hymenoptera and the biodiversity crisis, perhaps the most important relationship arising from my analyses is that both parasitoid community richness and host population dynamics may be influenced by common processes. The species richness of parasitoid communities and the ability of parasitoids to impact host populations are linked, and the proposed mechanism is the strength of refuges occupied by hosts. Whether or not refuges will ultimately be shown to be the primary mechanism operating remains to be seen. But, irrespective of the mechanisms that drive the relationship, an association of species richness and host regulation has important implications for arguments for the conservation of hymenopteran diversity. It has been suggested that the control of pests by biological control is enhanced by multiple parasitoid introductions (Huffaker *et al.*, 1971; DeBach, 1974). The rationale for this position is that several parasitoid species should produce higher overall host mortality levels than a single parasitoid species, or that several parasitoid species should be able to complement one another in different climatic conditions. Although my analyses do not directly test this, the correlation between parasitoid species richness and host mortality across hundreds of host–parasitoid complexes is consistent with this biological control philosophy. Turning the argument around, there is certainly no evidence that depauperate parasitoid communities typically produce higher host mortality levels. The obvious implication of this is that if during the mass extinction episode into which we may be moving parasitoids are more extinction prone than their herbivorous hosts, a loss of parasitoid diversity may well lead to a reduction in herbivore mortality. The ramifications of this to both natural and agricultural ecosystems are manifold (LaSalle and Gauld, 1992; LaSalle, this volume Chapter 8).

The focus of this chapter has been very much on broad patterns in parasitoid–host interactions. The identification of general patterns from diverse and disparate empirical observations is critical for generating testable theories concerning the constraints on biotic interactions (Price, 1991a). This is particularly important when resources are limited and choices have to be made as to where research efforts must be concentrated. The stunning diversity of parasitoids in general, and of the parasitic Hymenoptera in particular, as well as that of their insect hosts almost certainly precludes our ever having a complete record of all of the species involved or being able to document the detailed structure of each and every parasitoid–host system. On the other hand, a large body of

empirical work on parasitoid–host interactions has been built up over the past 75 years or so, and the current challenge is to organize this existing work into a conceptual framework. This chapter represents one such attempt. Although the data are incomplete, and all of the important patterns have not yet been identified, enough patterns in parasitoid–host interactions have been identified to allow us to attempt synthetic, conceptual theories (e.g. Price, 1991a, b). A great deal of work remains to be done, but we must be willing to take the broad view, while appreciating that the details are necessary for testing general principles and will have to be documented as well, as time permits. Without the search for general patterns it is exceedingly unlikely that an understanding of the interactions involving perhaps half of the world's multicellular species (plants, herbivores and their parasitoids) will be possible in the foreseeable future. Given the pressures now being exerted on biological communities by human activities and the lack of research funds and personnel to study them all, by the time that all of the relevant detailed data are available it may be too late.

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The Role and Enhancement of Parasitic Hymenoptera Biodiversity in Agroecosystems

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Introduction

Research on the diversity of parasitic Hymenoptera in agroecosystems has concentrated mostly on the study of parasitoid complexes attacking particular native as well as exotic pest species. Some pest species support a large number of parasitoid species, such as the hessian fly *Mayetiola destructor* (Say) (Gahan, 1933), the wheat-stem sawfly (*Cephus pygmeus* (L.) (Salt, 1931), the coconut beetle *Promecotheca caeruleipennis* Blanchard (Taylor, 1937), the bean gall sawfly *Pontania proxima* (Lepeletier) (Carleton, 1939) and the coffee leaf miner *Perileucoptera coffeella* (Guerin-Meneville) (Parra *et al.*, 1977; Aviles and Cure, 1990). Different crops support particular herbivore species, which, in turn, are attacked by one or several parasitoid species (Table 11.1), although such associations may change according to geographical location, management intensity and crop arrangements. In many cases, only one or two species of such complexes prove vital in the natural biological control of key insect pests. For example, in California's alfalfa fields, the braconid wasp *Apanteles medicaginis* Muesebeck plays a key role in regulating the numbers of the alfalfa caterpillar *Colias eurytheme* Boisduval. Apparently, this pristine butterfly-wasp system moved from native clovers into the new and artificial irrigated alfalfa fields (Hagen *et al.*, 1971). Similarly in North Carolina's tobacco fields, *Campoletis perdistinctus* (Viereck) exerts a high parasitization rate on the budworm *Helio-*

Table 11.1. Species richness of parasitoid complexes associated with different insect pests in a range of annual cropping systems.

Crop system	Pest species	No. of parasitoid species	Location	Reference
Cotton	<i>Spodoptera exigua</i> (Hübner)	11	California	van den Bosch and Hagen (1966)
	<i>Trichoplusia ni</i> (Hübner)	11	California	van den Bosch and Hagen (1966)
	<i>Heliothis zea</i>	14	California	van den Bosch and Hagen (1966)
	<i>Bucculatrix thurberiella</i> Busck	3	California	van den Bosch and Hagen (1966)
	<i>Estigmene acrea</i> (Drury)	3	California	van den Bosch and Hagen (1966)
	<i>Spodoptera praefica</i> (Grote)	13	California	van den Bosch and Hagen (1966)
Sorghum	<i>Schizaphis graminum</i> (Rondani)	3	USA	Young and Teetes (1977)
Cassava	<i>Erinnys ello</i> L.	4	Brazil, Colombia	Bellotti and Schoonhoven (1978)
	<i>Jatrophia brasiliensis</i> Rubs.	4	West Indies, Peru	Bellotti and Schoonhoven (1978)
	<i>Saissetia</i> sp.	2	Cuba	Bellotti and Schoonhoven (1978)
Soyabeans	<i>Plathypena scabra</i> (F.)	14	Missouri, USA	Turnipseed and Kogan (1976)
	<i>Pseudoplusia includens</i> (Walker)	12	Louisiana, USA	Turnipseed and Kogan (1976)
Potato	<i>Myzus persicae</i>	7	Maine, USA	Shands <i>et al.</i> (1965)
	<i>Acyrtosiphon solani</i> (Kattenbach)	5	Maine, USA	Shands <i>et al.</i> (1965)
	<i>Aphis nasturtii</i> Kattenbach	5	Maine, USA	Shands <i>et al.</i> (1965)
Rice	<i>Nephotettix</i> spp.	3	Philippines	Reissig <i>et al.</i> (1985)
	<i>Chilo suppressalis</i> (Walker)	5	Philippines	Reissig <i>et al.</i> (1985)
Alfalfa	<i>Colias eurytheme</i> Boisduval	2	California	Hagen <i>et al.</i> (1971)
	<i>Spodoptera exigua</i>	11	California	Hagen <i>et al.</i> (1971)
	<i>Spodoptera</i> (= <i>Prodenia</i>) <i>praefica</i> (Grote)	13	California	Hagen <i>et al.</i> (1971)
	<i>Heliothis zea</i>	13	California	Hagen <i>et al.</i> (1971)
Tobacco	<i>Heliothis virescens</i>	2	North Carolina, USA	Rabb (1971)

this virescens (F.), in early summer prior to flowering when plants are most susceptible to budworm injury. After flowering and on post-harvest sucker tobacco, parasitization by *Campoletis perdistinctus* declines and the action of *Cardiochiles nigriceps* becomes an important budworm mortality factor (Rabb, 1971). In other cases, it is a combination of several parasitoid species that exerts regulation on a specific insect pest (Ehler, 1990).

Our knowledge of naturally occurring or already established parasitoid communities in agroecosystems in general is not very sophisticated. One complication is that such communities are hard to define sharply because many parasitoid species enter the parasitoid complexes of more than one host, some of which may not be recognized as belonging to the same community (Askew and Shaw, 1985). Another complication is that Hymenoptera parasitoids are seldom monophagous; on the contrary they are polyphagous and more habitat and/or niche specific than host specific (Vinson, 1977). In fact, many parasitoid species are more likely to attack taxonomically unrelated insects found in one habitat than they are to attack taxonomically related insects occupying different habitats (Vinson, 1981).

In this chapter we discuss the pertinent literature concerned with the community structure, organization and development of parasitic Hymenoptera on agricultural systems, attempting to define trends and perspectives that may be useful to further understand parasitoid communities on crops. Although we know more about the factors that negatively impact parasitoid diversity, abundance and efficacy in agroecosystems (i.e. chemical insecticide applications, monocultures, tillage, etc.), we identify factors important in enhancing Hymenoptera parasitoid diversity, as well as management practices that add environmental resources necessary for improving parasitoid effectiveness in agroecosystems.

The complexity of Hymenoptera parasitoid communities in agroecosystems

Most of the studies on the composition of parasitoid complexes have been conducted on crop monocultures where host populations usually reach abnormal abundance levels (Askew and Shaw, 1985). To some researchers, such records either underestimate species diversity or represent what may be considered 'artificial' parasitoid communities. The relative complexity of Hymenoptera parasitoid communities associated with different cropping systems is determined by biological, environmental and management factors. In large-scale monocultures, diversity is suppressed by pesticides, vegetational simplification and other environmental disturbances. In less disturbed agroecosystems, in addition to the absence of pesticides, parasitoid diversity seems related to crop diversity, ground cover, weeds and native vegetation adjacent to crops. In fact, the few studies conducted on this topic indicate that the vegetational settings associated with particular crops influence the kind, abundance and time of arrival of parasitoids.

Based on the available information, it is possible to define the following

trends of Hymenoptera parasitoid diversity in agroecosystems:

1. *Parasitoid diversity decreases with intensity of agroecosystem management.* Surveys conducted in relatively unmanaged apple orchards revealed a high species richness of parasitic Hymenoptera (Table 11.2). In general, in pesticide-free orchards and/or in unmanaged or abandoned orchards, a wide range of parasitoid species is present. Over the span from unmanaged to intensively managed systems, a dramatic decrease in diversity and species composition occurs, in fact most natural enemies are eliminated (Fig. 11.1) (Croft and Hull, 1983). Although a usual outcome of intensive management is a reduction in the physical heterogeneity within the crop, parasitic Hymenoptera may exhibit a high degree of environmental heterogeneity within the same planted area. Four large plots sampled within the same *Eucalyptus cloeziana* reforested area in Brazil, showed almost 100% dissimilarity values between plots for parasitic Hymenoptera and Bethyloidea (Campos and Cure, 1991; Table 11.3). Sampled areas differed in the types of neighbouring vegetation; reforested plots closer to a natural forest reserve exhibited higher diversity than plots located away from the reserve.
2. *The parasitoid complexes of taxonomically and ecologically related pests found in the same crop but in widely separate areas are similar.* The major parasitoid species associated with the lepidopterous pests *Pieris* and *Plutella* and the

Table 11.2. Species richness of parasitic Hymenoptera inhabiting relatively unmanaged apple orchards in two locations.

Parasitic Hymenoptera	Number of species	
	Indiana	Wisconsin
<i>Dominant families</i>		
Eulophids	24	55
Pteromalids	16	37
Encyrtids	17	14
Braconids	30	36
Ichneumonids	15	34
Total:	102	176
<i>Dominant genera</i>		
<i>Tetrastichus</i>	7	10
<i>Sympiesis</i>	3	7
<i>Pteromalus</i>	2	6
<i>Apanteles</i>	6	6

Source: Alter Oatman *et al.* (1964) and Cleveland and Hamilton (1958).

Table 11.3. Dissimilarity measurements (chor distance index, minimum = 0, maximum = 1.41) for Hymenoptera-Parasitica and Bethyloidea between plots in a reforested *Eucalyptus* spp. area in Brazil.

Plot comparisons	Dissimilarity
A1 vs. A2	1.33
A1 vs. B1	1.27
A1 vs. B2	1.39
A2 vs. B1	1.31
A2 vs. B2	1.17
B1 vs. B2	1.31

Source: After Campos and Cure (1991).

The reforested area (approx. 33 000 ha) was in contact with a natural forest reserve (approx. 37 000 ha). A1 and A2 plots were located about 100 m from the natural reserve. B1 and B2 plots were located 10 km within the reforested area.

aphid *Brevicoryne brassicae* (L.) infesting cabbage in upstate New York and in Minnesota were similar. In both areas, *Diaeretiella rapae* (M'Intosh) was a prominent parasitoid of *B. brassicae*, and *Pieris rapae* (L.) was consistently attacked by *Apanteles glomeratus* (L.) (Pimentel, 1961; Weires and Chiang, 1973). The same parasitoids are prevalent in cole cropping systems throughout South America (Parker and Berry, 1951).

3. *Species diversity of parasitoids associated with hosts on tree crops is higher than with hosts on annual or herbaceous crops.* Orchards are semi-permanent and less disturbed systems than annual monocultures, therefore providing more stable habitats for parasitoid colonization and establishment. Orchards also provide a longer time-frame for the establishment of species associations and/or interactions (MacArthur, 1965). Apple orchards in Wisconsin supported about 176 species of parasitic Hymenoptera whereas in Maine only 22 parasitoid species were associated with the pest complex (mostly aphids) attacking potatoes (Oatman *et al.*, 1964; Shands *et al.*, 1965). Although this comparison may not be totally appropriate, because areas are geographically separate and systems were probably subjected to different management techniques, it highlights the tremendous disparity in parasitoid species diversity associated with a perennial crop versus an annual crop.

Annual monocultures are continuously disturbed and also create unfavourable microclimates for many parasitoids. Ichneumonid species tend to be excluded from systems that lack cool and moist conditions, such as those often prevalent in monocultures in lowland tropical areas and in the Central Valley of California (Townes, 1971).

4. *The colonization of crops by parasitoids is correlated with the pattern of habitat space development in crop systems.* With time, both quantitative and qualitative changes occur in crop habitats which, in turn, affect the structure and organization of the arthropod community. As the season progressed, the

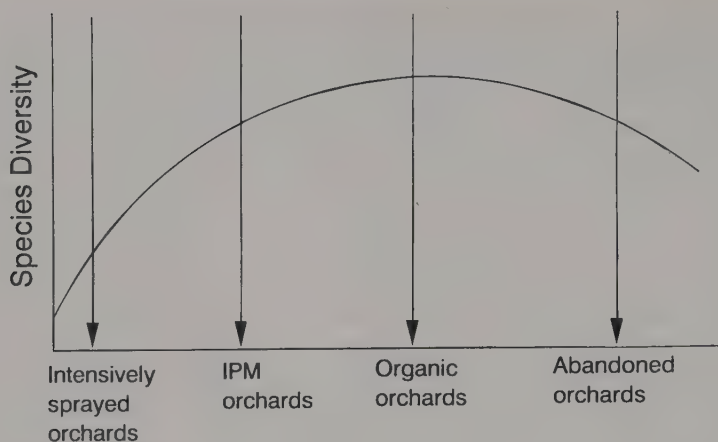


Fig. 11.1. Hypothetical trend in parasitic Hymenoptera species diversity in a range of apple orchards subjected to various degrees of management intensity (based on Croft and Hull, 1983).

complexity of the arthropod food web increased in Illinois soyabean fields (Mayse and Price, 1978). A similar trend was observed in pear orchards as trees developed (Gut, 1985). Over long time periods in tea plantations, species richness increased and guild structure changed with tree age (Banerjee, 1983).

5. *Plant species diversity and plant structural diversity are important in determining parasitoid diversity in agroecosystems.* As plant complexity increases in agroecosystems in the form of intercropping, cover crops, living mulches, wind-breaks, etc., insect species diversity also increases. In California, Brussels sprouts monocultures supported only three parasitoid species, whereas Brussels sprouts intercropped with fava beans and/or wild mustards supported five and eight species respectively (Altieri, 1984). In tropical Mexico, malaise trap captures of parasitic Hymenoptera in squash monocultures consisted of fewer individuals and were characterized by a lower parasitoid species richness than those from corn-bean-squash polycultures (Letourneau, 1987; Fig. 11.2). In the polycultures, four braconid species and one ichneumonid species were consistently associated with the main herbivore *Diaphania hyalinata*, exerting higher parasitization rates than in the monoculture. In their survey of soyabean fields, Mayse and Price (1978) found higher numbers of parasitoid species per habitat space in rows located at the edge of a field adjacent to relatively complex vegetation than in the rows located away from the neighbouring vegetation.

Enhancing parasitic Hymenoptera diversity in agroecosystems

There are several environmental factors that influence the diversity, abundance, survival and activity of parasitoids in agroecosystems: microclimatic conditions,

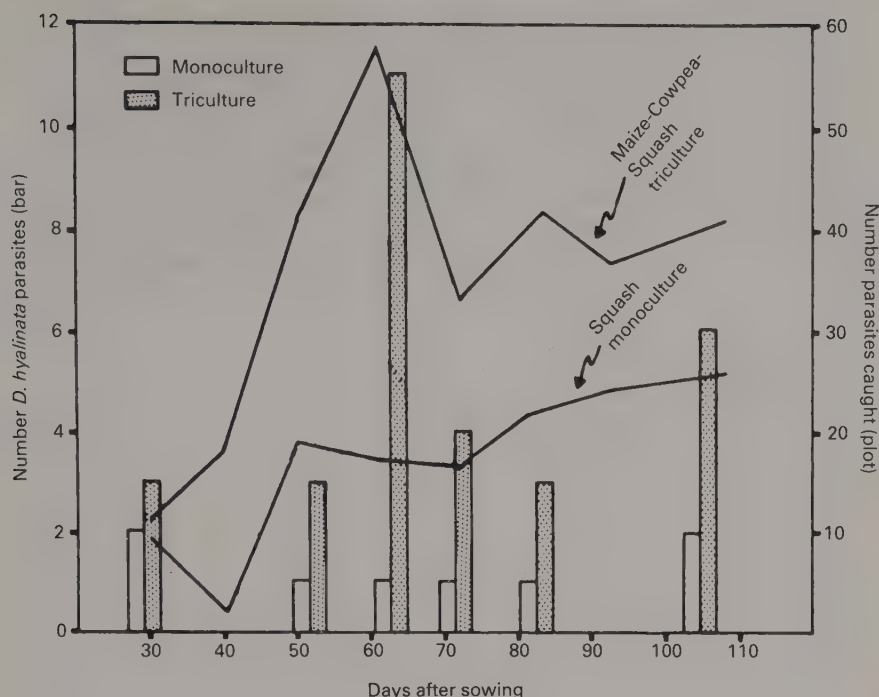


Fig. 11.2. Total number of parasitic Hymenoptera (line plot) and the number of species known to parasitize *Diaphania hyalinata* in squash monocultures and maize-bean-squash tricultures in tropical Mexico (Letourneau, 1987).

availability of food (water, hosts, pollen and nectar), habitat requirements (refuges, nesting and reproduction sites, etc.), intra- and inter-specific competition and other organisms (hyperparasites, predators, humans, etc.). The effect of each of these factors will vary according to the spatial and temporal arrangement of crops and the intensity of crop management. Since agroecosystems are dynamic and subjected to different kinds of management, crop mixes continually change in the face of biological and socio-economic factors. Such landscape variations determine the degree of spatial and temporal heterogeneity characteristic of agroecosystems, which, in turn, may or may not benefit parasitic Hymenoptera diversity in specific cropping systems.

Although parasitoids seem to vary widely in their response to crop distribution, density and dispersion, experimental evidence suggests that structural (i.e. spatial and temporal crop arrangement) and management (i.e. crop diversity, input levels, etc.) attributes of agroecosystems influence parasitoid diversity and dynamics. Based on the available information, parasitoid diversity can be enhanced and effectiveness improved in the following ways (van den Bosch and Telford, 1964; Rabb *et al.*, 1976; Altieri and Letourneau, 1982; Powell, 1986):

Table 11.4. Number of parasitic Hymenoptera species introduced and established as biological control agents for arthropod pests in forests and agroecosystems. The degree of success ranges from zero (no control), to 3 (excellent control) and is based on the arithmetic mean calculated for registered cases classified as: zero = no economic control; 1 = control in a limited part of the distribution range; 2 = control in a substantial part of the distribution range; 3 = excellent control throughout; ? = implies uncertain establishment of the parasite.

Family	Number of species	Number of target species	Number of crop species	Degree of success
Aphelinidae	46	30	13	2.1
Bethylidae	1	1	1	?
Braconidae	66	60	40	1.5
Chalcididae	5	7	13	0.3
Diapriidae	1	1	8	?
Dryinidae	2	1	1	1.0
Encyrtidae	134	44	41	1.0
Eulophidae	25	40	36	1.1
Eupelmidae	2	2	2	1.0
Ibaliidae	1	1	1	0.0
Ichneumonidae	42	30	18	1.2
Mymaridae	7	6	8	1.6
Platygasteridae	5	5	6	2.7
Pteromalidae	13	11	11	1.4
Scelionidae	10	8	8	2.1
Scoliidae	11	6	4	1.3
Sphecidae	1	1	1	3.0
Tiphiidae	4	4	3	1.2
Torymidae	2	3	3	2.0
Trichogrammatidae	9	7	7	0.3

Source: Based on Luck (1981).

1. *Multiple introductions of parasitoids.* Importation of parasitoids has been used since 1906 as a strategy to reach long-term suppression of pests. The practice of classical biological control could be regarded as a global experiment in restoring natural enemy biodiversity in agroecosystems where exotic insects reach pest status because they have been introduced from a geographical distance without their regulating natural enemies. According to Greathead (1986) there are records of 860 successful establishments of 393 species of parasitoids against some 274 pest insects in 99 countries. In many of these cases, introduction of some 250 species of hymenopterous parasitoids have been rated as achieving satisfactory pest suppression in either a limited or substantial part of the pest's distribution range (Table 11.4). Hymenopterous parasitoids were also aided by introduction of other parasitoid or predator species to achieve a useful reduction

Table 11.5. Elimination of Hymenoptera parasitoids by insecticides sprayed to control key pests in a range of cropping systems.

Crop	Location	Pest species	Parasitoid species eliminated	Insecticide
Peach	Ohio	Oriental peach moth	<i>Macrocentrus ancyllivorus</i> Rohwer	DDT
Apple	Washington State	Woolly apple aphid	<i>Aphelinus mali</i> (Haldeman)	DDT
Apple	Washington State	Comstock mealybug	<i>Pseudaphycus</i> spp.	DDT
Citrus	Florida	Florida red scale	<i>Pseudhomalopoda prima</i> Girault	DDT
Citrus	California	Yellow scale	<i>Comperiella bifasciata</i> Howard	DDT
Citrus	California	Brown scale	<i>Metaphycus luteolus</i> (Timberlake)	Parathion
Cabbage	England	Cabbageworm	<i>Cotesia rubecula</i>	DDT
Citrus	Chile	Whiteflies	<i>Amitus spiniferus</i> (Brethes) and <i>Cales noacki</i> Howard	Organophosphates
Grapes	Chile	Mealybug	<i>Pseudaphycus flavidulus</i> Bohart	Organophosphates

Source: Brown (1978).

in pest numbers (Ehler, 1990). This fact gives support to the multiple-species introduction strategy (MSI) in classical biological control. Long time practitioners such as Huffaker *et al.* (1971) have already argued in favour of MSI and have stated that 'importation of a diverse complex of natural enemies is the only practical manner of obtaining the best species for a given habitat, or the best combination for such habitat, or the best combination for the entire host range'. Clearly, enhancing or restoring natural enemy biodiversity through importation assures a better chance of success than single species introduction; the challenge is determining which species or combination of species to introduce in order to control a given target species in a specific situation (Ehler, 1990).

2. Reducing direct mortality. The use of chemical pesticides has often created complex and serious problems by immediate and time-lag effects on natural enemies. Non-selective insecticides have created pest problems by eliminating parasitoids. DDT and parathion have been particularly deleterious to various parasitoids in several agroecosystems (Table 11.5).

Organophosphorus insecticides such as azinphosmethyl, parathion, diazinon, dimethoate and malathion are particularly toxic to hymenopterous parasites of citrus scales and mealybugs (Brown, 1978). Total removal of pesticides can restore parasitoid diversity and lead to renewed biological control of specific pests. Within two years, virtually all banana insect pests in Golfito, Costa Rica dropped to below economic threshold levels, due to enhanced parasitization and predation, after stopping insecticide (dieldrin and carbaryl) sprays (Stephens, 1984). Similarly, in California's walnut orchards, natural biological control of the frosted scale and the calico scale was soon achieved by encyrtid parasitoids after removal of DDT sprays (Hagen *et al.*, 1971).

Some cultural practices can also negatively impact parasitoids. Ploughing and cultivation generally inflict heavy mortality on natural enemies. Pruning, harvesting and crop residue disposal may also have effects on parasitoids. Removal of prunings of apple wood infested by the woolly aphid, but heavily parasitized by *Aphelinus mali* (Haldeman) in Australia, reduced parasitization levels within the orchard (Wilson, 1966). In California, solid harvesting of alfalfa was more devastating to the parasitoid *Aphidius smithii* Sharma and Rao than to its aphid host, *Acyrtosiphon pisum* (Harris). Conversely, strip harvesting resulted in an improved microclimate for the parasite (van den Bosch and Telford, 1964). It is not clear whether burning of sugarcane biomass is negative to the parasites of *Diatraea saccharalis* (F.).

3. Provision of supplementary resources. Most parasitoids have resource requirements such as hosts, food other than hosts, water, refuges, etc., which often are not available or found in sufficiency within a given cropping system. Several researchers have demonstrated that manipulating such resources can enhance parasitoid diversity and abundance and also improve their efficacy (Rabb *et al.*, 1976). Addition of host populations proved effective in controlling *Pieris rapae* in cabbage. The continuous release of fertile *Pieris* butterflies increased the pest

population nearly tenfold above normal spring populations, enabling the parasites *Trichogramma evanescens* Westwood and *Cotesia rubecula* (Marshall) to increase early and maintain themselves at an effective level throughout the season (Parker and Pinnell, 1972).

4. *Increasing adjacent vegetational diversity.* Researchers are well aware of the importance of adjacent vegetational settings in determining the diversity of parasitoid species as well as their maintenance and effectiveness within agroecosystems (van den Bosch and Telford, 1964; Altieri and Letourneau, 1982, 1984). Successful colonization by parasites depends upon the presence of the appropriate kind and abundance of primary hosts, alternative hosts, pollen and/or nectar in hedgerows and other neighbouring habitats. For example, in Armenia, scelionid egg parasites of the sunn pest *Eurygaster integriceps* Puton are very efficient in areas with small wheat fields surrounded by diverse vegetation. Under these conditions, the polyvoltine egg parasites have a number of other pentatomid hosts and favourable hibernating places. In California, Doutt and Nakata (1973) found that the egg parasite *Anagrus epos* Girault, was effective in controlling the grape leafhopper *Erythroneura elegantula* Osborn, in vineyards adjacent to wild blackberries which harbour a non-economic leafhopper *Dikrella cruentata* Gillette, whose eggs serve as the only overwintering resource for *Anagrus*. Also in California, Allen and Smith (1958) found that parasitization of the alfalfa caterpillar, *Colias eurytheme*, by *Apanteles medicaginis* was far greater in California's San Joaquin Valley where weeds were in bloom along irrigation canals in contrast to areas where the weeds were destroyed.

In England, the proximity of certain flowering weeds such as *Angelica sylvestris* L., *Urtica dioica* L., *Rumex acetosella* L., *Taraxacum officinale* Weber, *Cirsium vulgare* (Savi) Ten., *Ranunculus repens* L., *Trifolium repens* L., *Chenopodium album* L. and *Anthriscus sylvestris* L. increased the activity of parasitic Hymenoptera in wheat and cabbage fields (Van Emden, 1962).

The high degree of environmental heterogeneity found by Campos and Cure (1991) (Table 11.3) was partly explained by the fact that the 33 000 ha *Eucalyptus* reforested area was adjacent to a 37 000 ha natural forest reserve. Apparently, connections with natural reservoirs are important, and larger repositories can contribute more to species richness than smaller ones, the latter serving mostly as corridors.

5. *Increasing within-field plant diversity.* Considerable work in the former USSR has been devoted to the use of nectar-bearing plants within orchards as a source of adult food for entomophagous insects to increase their effectiveness. Field experiments of Chumakova (1960) in the North Caucasus showed that the growing of *Phacelia* spp. in orchards greatly increased the parasitization of *Quadraspidiotus perniciosus* (Comstock) by its parasite *Aphytis proclia* (Walker). These same plants have been shown to increase the abundance of the wasp *Aphelinus mali* for the control of apple aphids and improve the activity of *Trichogramma* spp. in apple orchards (Chumakova, 1977).

Spectacular parasitism increase was observed in apple orchards with rich undergrowths of wild flowers. Parasitism of tent caterpillar eggs and larvae and codling moth larvae was 18 times greater in those orchards with floral undergrowths than in orchards with sparse floral undergrowth (Leius, 1967).

Mixed cropping can also enhance parasitoids in crops. In Costa Rica, inter-crops of corn and sweet potatoes had 75% more species of parasitic Hymenoptera than corresponding monocultures (Carroll, 1978). Parasitism of the leafhopper *Empoasca kraemeri* Ross and Moore by the egg parasitoid *Anagrus* sp. was greater on beans grown associated with corn than on bean monocultures (Altieri *et al.*, 1978). Similarly, artificially placed *Heliothis zea* (Boddie) eggs were more heavily parasitized by *Trichogramma* wasps in corn-soyabean polycultures than in soyabean monocultures (Altieri and Todd, 1981). In Peru, planting rows of corn every fifth or seventh row of cotton favoured the reproduction of many predators and parasitoids (Beingolea, 1957).

It has been suggested that in some cases increased plant diversity could reduce parasitoid efficiency, since certain associated plants may mask cues used by parasitoids for host searching (Price *et al.*, 1980).

6. *Controlling secondary enemies.* The diversity and abundance of primary parasites can be greatly reduced by secondary (hyper) parasites. Several attempts to establish introduced parasites were frustrated by the presence of hyperparasites. In Nova Scotia, hyperparasites destroyed founder colonies of *Aphidius smithii* Sharman and Rao introduced for control of the pea aphid (Mackauer, 1972). In California, the effectiveness of *Diaeretiella rapae* against cabbage aphids in cole crops is negatively affected by species of *Asaphes* and *Pachyneuron*. In potato fields in Maine, 17 species of primary parasites and 18 species of hyperparasites were reared from the aphid complex. At times the hyperparasites *Asaphes lucens* (Provancher) and *Coruna clavata* Walker substantially reduced the abundance of the primary parasite *Aphidius nigripes* Ashmead, allowing populations of the potato aphid to flourish (Shands *et al.*, 1965). As pointed out by Greathead, (1986), the highly effective genus *Aphytis* is the only one among the successful parasitoids of Coccoidea that develops as an external parasitoid, thus avoiding hyperparasitism.

7. *Manipulating host plant attributes.* Several chemical, genetic and architectural attributes of plants can influence parasitoid action on insect pests. Rabb and Bradley (1968) found that parasitization of *Manduca sexta* (L.) eggs by *Trichogramma minutum* Riley and *Telenomus sphingis* (Ashmead) was inhibited by sticky exudates of tobacco leaves. *Encarsia formosa* Gahan, a normally effective parasitoid of the greenhouse whitefly, is greatly hindered by the hairs produced by cucumber (Price *et al.*, 1980).

It is also known that the nature of the host plant habitat affects the degree of parasitization obtained from certain parasitoids. In northern Florida, parasitization rates of *Heliothis* spp. and Plusiinae eggs by *Trichogramma pretiosum* Riley showed considerable variation in various crops grown in the same field (Martin

% PARASITIZATION OF EGGS
BY *TRICHOGRAMMA* SPP.

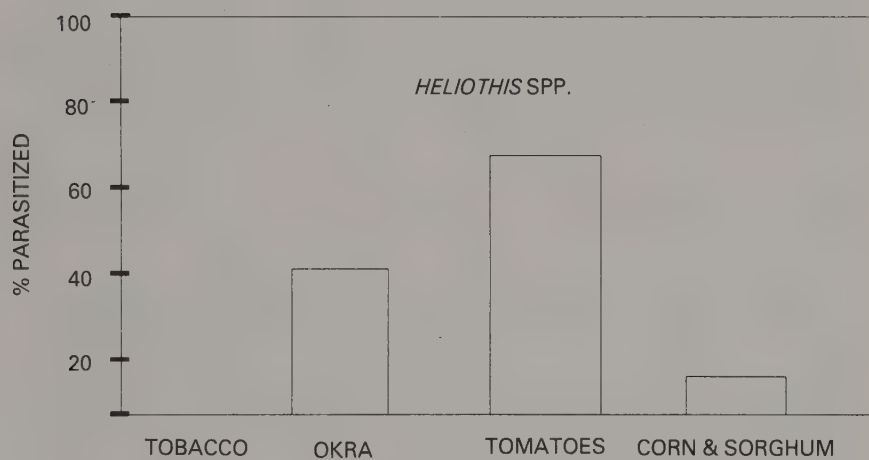
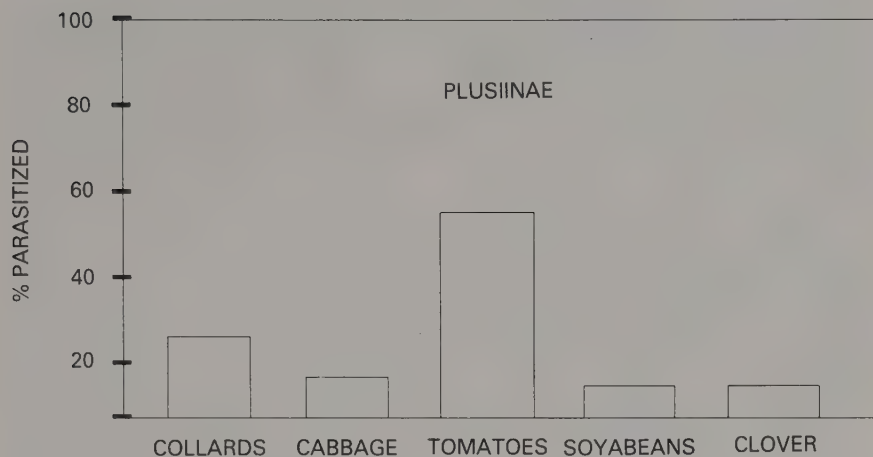


Fig. 11.3. Parasitization of *Plusiinae* eggs and *Heliothis* spp. by *Trichogramma* spp. populations in various crop systems in north Florida (Martin *et al.*, 1976).

et al., 1976). Moderate to high rates of parasitization were attained in tomatoes, collards and okra. The released parasites were ineffective against the target pests in tobacco (Fig. 11.3). Although these differences could have been due to differences in host egg densities, various chemical and physical cues emitted by the different crops were significant in affecting the location of the host habitat by *Trichogramma* wasps. Similar results were obtained in New York State where para-

sitism by *Diaeretiella rapae* was much higher when the aphid *Myzus persicae* (Sulzer) was on collard than when it was on beet (Read *et al.*, 1970).

Some parasitoids specialize their search to specific plant organs or even parts of an organ. For example, Gold *et al.* (1989) found significantly lower rates of parasitism of cassava hornworm eggs by *T. sphingis* on lower leaf surfaces than on the upper leaf surfaces. Other parasitoids will have differential rates of attack on the same host but inhabiting different plant species. Apple maggots that feed on apples are less often parasitized by *Biosteres melleus* (Gahan) than when they feed on hawthorn fruits (Porter, 1928).

Alkaloids and other allelochemicals involved in plant resistance can be toxic to parasitoids within hosts. The effects of tomatine on the larval development of the ichneumonid *Hyposoter exiguae* (Viereck) illustrates how toxins derived from plants by herbivores can affect parasitoid survivorship (Campbell and Duffy, 1979). Smith (1957) found high larval mortality of two parasitoids of the California red scale, when the scale fed on sago palm compared to when it fed on citrus.

Resistant varieties can have negative effects on natural enemies. The smaller sized hosts on resistant varieties can lead to the emergence of smaller parasitoids having reduced fecundity. According to Van Emden (1991) these disadvantages disappear at low levels of plant resistance.

8. *Manipulations with semiochemicals.* Chemicals which stimulate host-searching behaviour in parasitoids have been identified for a number of Hymenoptera species: *Cardiochiles nigriceps*, *Trichogramma evanescens*, *T. pretiosum*, *Trissolcus* sp., *Telenomus* sp., *Microplitis croceipes* and *Aphidius nigripes* (Nordlund *et al.*, 1981). Hexane extracts sprayed in field trials have consistently improved parasitization rates of *H. zea* eggs by *T. pretiosum*. The greatest utility of such kairomonal applications appears to be for aggregating or retaining released parasites in target locations (Lewis and Nordlund, 1985).

Taking advantage of the fact that many parasitoids seek out particular habitats and are guided by volatiles emanating from plants, some researchers have applied certain plant extracts on crop plants to reinforce the host location behaviour of parasitoids and have improved parasitization rates (Altieri *et al.*, 1981). Spraying of plant-produced synomones attracted ovipositioning female parasitoids, enhancing the parasitization of *H. zea* and *Anagasta kuehniella* (Zeller) by *Trichogramma* wasps under soyabean field and greenhouse conditions respectively (Altieri *et al.*, 1981; Altieri and Letourneau, 1982). Similar results were obtained by Titayavan and Altieri (1990) in broccoli plots. Direct application of an allylisothiocyanate emulsion at a rate of 0.25 ml per broccoli plant consistently gave higher parasitization rates of the cabbage aphid and/or number of *Diaeretiella rapae* wasps per plant, than those observed on plants treated with 0.25 ml of water or with 0.25 ml of wild mustard extract.

Conclusions

Agroecosystems are complex and dynamic systems subjected to a whole range of vegetational designs and management intensities depending on farmers' preferences, environmental factors and socio-economic constraints. Changes in plant diversity, plant density, crop dispersion and patch size will increase or reduce resources for natural enemies. Therefore, the size and structure of parasite Hymenoptera communities should be expected to vary according to the heterogeneity of specific agroecosystems.

When considering ways of enhancing parasitoid diversity and efficiency, what is difficult is that each agricultural situation must be assessed separately. Diversified vegetational settings will generally result in enhanced diversity and abundance of parasitoids, although specifically which species will be enhanced will vary depending on the diversity and availability of primary and alternative hosts, location and size of the field, plant composition, floral diversity and phenology, surrounding environments and management technologies. One can only hope to elucidate the basic ecology of parasitoids, their relationships with other components of the agroecosystem and the ecological principles governing parasitoid diversity in crop fields. In this regard, manipulating agroecosystem components (habitat diversity, pesticide-free space, alternative food, semiochemicals, etc.) to provide the basic requirements needed by parasitoids (hosts, pollen and nectar, refuges, reproduction and nesting sites, etc.) is an effective way to apply ecological theory to improve parasitoid diversity and efficiency in agriculture.

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Spatial Patterns in the Description and Richness of the Hymenoptera

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Introduction

Described species are neither a random nor, in any sense, a statistically representative sample of the global insect fauna. Proportions of species that have been described are greater in some taxa and in some regions than in others. Virtually no taxa have been described in their entirety, and for most taxa the faunas in most regions are incompletely known. Growing concern over the impending loss of a substantial portion of the world's fauna and flora has served to highlight this situation.

If rational decisions are to be made as to how best to avert or minimize the 'biodiversity crisis', sound data on patterns of species richness, species distributions and species evolutionary relationships are required (Roberts, 1988; Howarth and Ramsay, 1991; Lubchenco *et al.*, 1991; Sutton and Collins, 1991; Vane-Wright *et al.*, 1991). The database of species descriptions for most groups of insects is woefully inadequate for this task. In consequence, there have been repeated pleas for a rapid expansion in the numbers of described species, and also for descriptive and classificatory areas of taxonomic work to prioritize particular groups and regions for study (e.g. Wilson, 1985a, b, 1988; Wolf, 1987; Soulé, 1990; Wheeler, 1990).

Justifications for an increase in species descriptions can be made not only on the imperative of conservation, but also, for example, on heuristic and economic grounds. Curiously, however, arguments for an enlarged and more focused body of species descriptions have rarely progressed beyond the expression of the general need for such work.

There has been little detailed consideration of current patterns of description, how these relate to actual patterns of species richness, and how the gap between the two might most profitably be closed. In this chapter I examine the present geographical patterns of species descriptions in the Hymenoptera, and how these might relate to the probable distribution of the group's global fauna. Some of the lessons which might be drawn from such a comparison are identified.

This study is based in large part upon data in the volumes of *Zoological Record* covering the period 1984–89 on the numbers of species of Hymenoptera recorded as newly described from different regions. These figures do not strictly simply refer to species described over these six years, but are sufficiently close that they will, for ease of reference, be treated as though they did. These figures also refer only to the numbers of newly described species having type localities in a particular region. Type localities do not, of course, perfectly reflect patterns of species distribution nor even collection. Series of specimens of a particular species sometimes comprise individuals from several regions, and numerous reasons might determine which specimen is designated as the type. However, for the purposes of ascertaining broad patterns of taxonomic effort such complexities are not important.

It is clear that across the whole of the Hymenoptera there is no single and uniformly applied definition of what constitutes a species. Thus summing the numbers of species from different groups is somewhat like adding apples and oranges. For present purposes, however, I take the pragmatic approach of simply accepting species concepts as currently applied by workers on different groups. In terms of establishing basic patterns of hymenopteran species richness, described or otherwise, it seems more useful to rely upon presently recognizable taxonomic units than to be too concerned about their strict comparability or the numbers of 'cryptic' species they may hide.

The spatial unit used throughout this study is primarily that of the country. This is not because it has any particular merit in terms of understanding patterns in taxal richness, but rather because it is the unit for which the most information is available. It is also the scale at which it may be easiest to engender changes in levels of descriptive effort.

The Distribution of Species Descriptions

Somewhat less than 8000 species of Hymenoptera were recorded as newly described over the period 1984 to 1989. Their type localities were distributed among the world's nations in a highly skewed fashion (Fig. 12.1). The largest number of species was described from the territory of the USSR, followed by the USA, and these two areas alone accounted for more than 20% of descriptions. Only 19 nations each contained the type localities of more than 100 species, but in sum these accounted for almost 70% of species described (Table 12.1). The

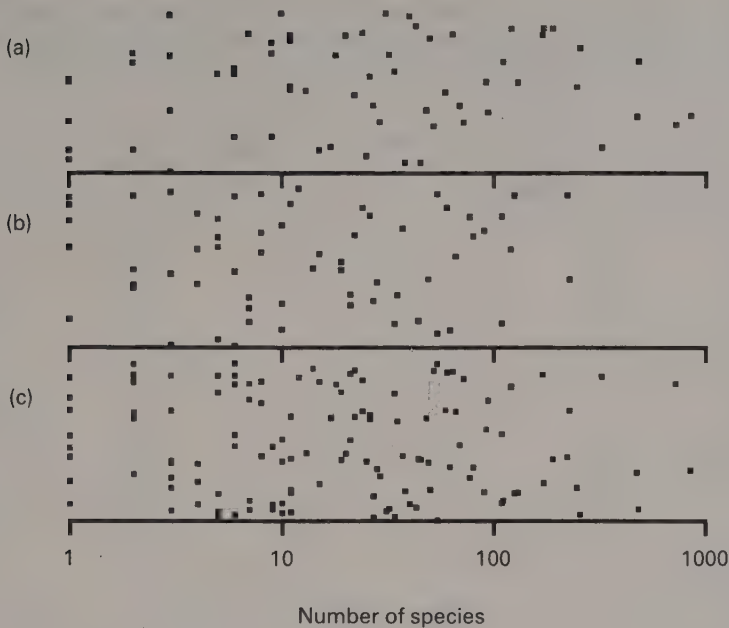


Fig. 12.1. Distributions of the numbers of species described from each country having an area in excess of 10000 km². These are presented as jitter plots, each dot represents a country, its position on the x-axis gives the number of species described, while its position on the vertical axis is random. Note that the x-axis is on a logarithmic scale. (a) Temperate nations (see text for definition). (b) Tropical nations. (c) All nations.

other 30% were distributed among more than 100 further nations of more than 10000 km² in area (Fig. 12.1), as well as many smaller ones.

The number of species of Hymenoptera in regional assemblages undoubtedly increases towards lower latitudes, through a product of increasing levels both of local richness and of species turnover (beta diversity). This pattern has, however, been very poorly documented, and it is impossible at present to suggest by what factors 'typical' temperate and tropical regional assemblages might differ in species richness. Indeed, most information is available for taxa which have extra-tropical peaks in richness (e.g. Michener, 1979; Janzen, 1981; Gauld, 1986). None the less, it is plain that patterns of species description do not reflect the overall latitudinal increase in richness. Of the nations from which more than 100 species were described between 1984 and 1989, only six might be regarded as truly tropical, and none of these appears among the nations with the highest numbers of descriptions. Defining tropical nations crudely as those having 50% or more of their land area within 20°N and 20°S, it is apparent that the distributions of descriptive effort among both temperate and tropical nations separately

Table 12.1. The countries from which more than 100 species of Hymenoptera were recorded as described in *Zoological Record* for the six years 1984–89, and the proportion of the total number of descriptions over this period which they account for.

	% of total
USSR	11.0
USA	9.4
Australia	6.3
India	6.2
China	4.2
Japan	3.3
Taiwan	3.2
Brazil	3.0
Papua New Guinea	2.9
South Africa	2.5
Mexico	2.2
Canada	2.2
Argentina	1.7
Philippines	1.6
New Zealand	1.6
Costa Rica	1.6
Mongolia	1.4
Malaysia	1.4
Zaire	1.4

are similar to the patterns for the two groups combined (Fig. 12.1); the majority of nations have few described species, while a few have many.

'Megadiversity' Countries

Largely on the basis of data for well-known animal and plant taxa, it has been suggested that at least 60–70% of the world's species occur in just 12 particular nations (see Table 12.2 for list; McNeely *et al.*, 1990, and references therein). It seems highly probable that these same nations also harbour the bulk of hymenopterian species. The demonstration that spatial patterns of hymenopterian species description do not track real patterns of species richness is thus reinforced by the fact that in sum the 'megadiversity' nations contributed only about 30% of the species described between 1984 and 1989 (Table 12.2). Only seven of the 12 had more than 100 species described from them over this period.

Table 12.2. The 'megadiversity' nations, as listed by McNeely *et al.* (1990), and the proportions of the total number of Hymenoptera descriptions over the 1984–89 period which they account for.

	% of total
Australia	6.3
India	6.2
China	4.2
Brazil	3.0
Mexico	2.2
Malaysia	1.4
Zaire	1.4
Indonesia	1.2
Colombia	1.0
Peru	0.8
Madagascar	0.8
Ecuador	0.7
Total	29.2

Area Effects

So far the effects of land area upon the numbers of species described from a country have been ignored. None the less, it might reasonably be expected that more species would on average be described from larger countries, for the simple reason that species richness is a positive function of area (MacArthur and Wilson, 1967; Williamson, 1988). Indeed, this is so, more species of Hymenoptera were described from larger nations during the 1984–89 period than from smaller nations (Fig. 12.2). The relationship is relatively weak, with area only explaining some 25% of the variance in the numbers of species of Hymenoptera described from different countries. This could potentially be explained on the grounds that tropical countries tend to have greater numbers of species per unit area than temperate ones, and this plot includes both temperate and tropical countries. However, as already apparent, differences in the actual numbers of species of Hymenoptera in temperate and tropical nations are not reflected in the numbers of described species. Differentiating temperate and tropical nations as before, we find that no more species were described from tropical nations per unit area than from temperate nations (Fig. 12.2). This might actually mean that the amount of effort being directed towards describing temperate species is greater than that directed towards tropical ones. Temperate faunas are already proportionately far better known than tropical ones, so it is actually that much more difficult to *find* previously undescribed species in the former than in the

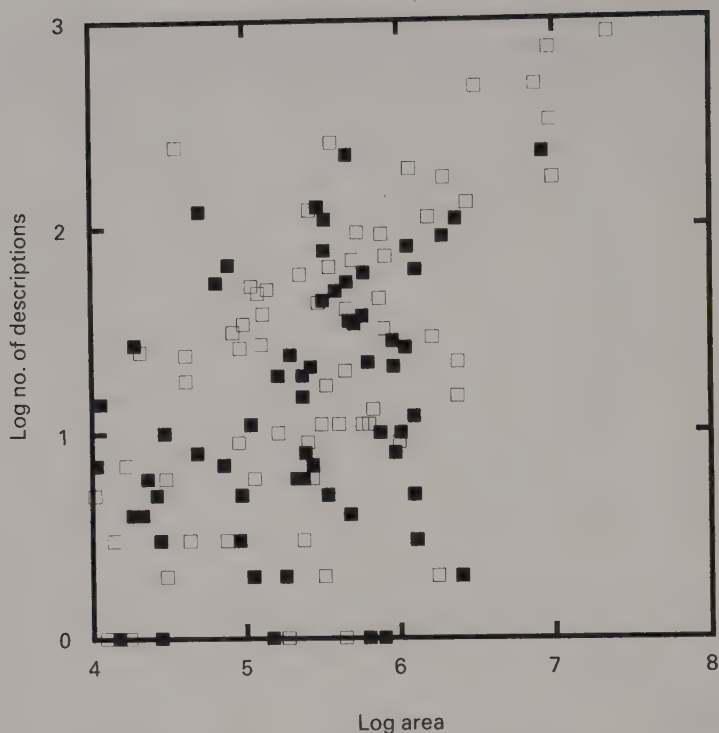


Fig. 12.2. Relationship between the numbers of species described from the various nations with areas in excess of 10 000 km² and the areas of those nations. Both axes are log transformed. Open symbols are for temperate nations and closed for tropical (see text for definitions). $r = 0.499$, $n = 128$, $P < 0.001$.

latter (although in the better worked groups it may perhaps be easier to recognize and hence describe new species in temperate regions).

Biogeographic Regions

Based on other taxa, it seems reasonable to suppose that perhaps a quarter to a half of extant species of Hymenoptera are found in the Neotropics, somewhat fewer in the Indotropics and still fewer in the Afrotropics (arguably this pattern tends to parallel the relative net primary productivities (Uchijima and Seino, 1987) of these regions). Less than 20% of species of Hymenoptera are likely to be found only outside of tropical realms. Estimates for some major groups of Hymenoptera of the proportions of their species which occur in various biogeographic regions lend some support for these statements (Table 12.3). However,

Table 12.3. Approximate proportions of global species numbers in some hymenopteran groups estimated to occur in different biogeographic regions. Nea = Nearctic, Neo = Neotropics, Eth = Ethiopian, Mad = Madagascar, Aus = Australia. Note, figures for the different taxa are not necessarily strictly comparable. Those for Chalcidoidea are based on much higher levels of faunal overlap than are the other figures.

	Nea	Neo	Eth	Mad	Aus
Chalcidoidea	0.15	0.50	0.30	0.15	0.15
Ichneumonidae	0.13	0.33	0.13	0.03	0.03
Formicidae	0.04	0.20	0.16	0.03	0.13
Vespidae ¹	0.07	0.36	0.18	0.03	0.09

Sources: personal communications from B. Bolton, J.M. Carpenter, I.D. Gauld, J.S. Noyes.

¹Including Masarinae and Eumeniinae.

because hymenopteran faunas are not being sampled in relation to their actual species richness, once again these patterns are not found in the distribution of the numbers of species being described from the different regions (Table 12.4). Rather, largely because they are of greater extent (but see above), more species were described from the various temperate biogeographic regions than from the tropical ones.

Table 12.4. The proportion of the total number of species of Hymenoptera described over the 1984–89 period from different biogeographic regions, the area (thousands of sq. km) and the numbers of species described per unit area of those regions.

	% of total	Area	Spp./area
Nearctic	13.8	23417	0.045
Neotropical	12.8	18791	0.053
Palearctic	24.4	40084	0.047
Ethiopian	10.3	22326	0.035
Madagascar	0.8	594	0.103
Indian subcontinent	8.1	5000	0.125
China, Japan and Taiwan	11.8	11711	0.077
Thailand to New Caledonia	9.6	4769	0.155
Australia and Tasmania	6.3	7682	0.063
New Zealand	1.6	265	0.457
Oceanic islands	0.5	—	—

Table 12.5. Numbers of species described (or known) in each of the families of Hymenoptera. Higher classification follows LaSalle and Gauld (this volume Chapter 1).

Hymenopteran families	Species described/ known	Hymenopteran families	Species described/ known
Symphyla		Proctotrupeoidea	
Xyeloidea		Peleciniidae	}
Xyelidae	56	Vanhorniidae	
Megalodontoidea		Roproniidae	
Pamphiliidae	232	Peradeniidae	
Megalodontidae	70	Heloridae	
Tenthredinoidea		Austroiniidae	}
Blasticotomidae	9	Monomachidae	
Argidae	812	Proctotrupidae	310
Cimbicidae	131	Diapriidae	2242
Diprionidae	125	Platygasteroidea	
Tenthredinidae	3840	Scelionidae	2922
Pergidae	411	Platygasteridae	1100
Siricoidea		Cynipoidea	
Siricidae	87	Ibaliidae	10
Xiphydriidae	94	Liopteridae	80
Anaxyelidae	1	Figitidae	300
Orussoidea		Eucoilidae	1000
Orussidae	69	Cynipidae	1700
Cephoidea		Charipidae	200
Cephidae	79	Chalcidoidea	
Apocrita		Leucospidae	134
Trigonalynoidea		Chalcididae	1466
Trigonalynidae	70	Eurytomidae	1201
Megalyroidea		Torymidae	889
Megalyridae	<100	Agaonidae	608
Evanioidea		Ormyridae	66
Evaniidae	400	Eucharitidae	348
Aulacidae	150	Perilampidae	229
Gasteruptiidae	500	Pteromalidae	3003
Stephanoidea		Eupelmidae	715
Stephanidae	>100	Tanaostigmatidae	88
Ceraphronoidea		Encyrtidae	3277
Megaspilidae	448	Tetracampidae	44
Ceraphronidae	354	Aphelinidae	975
		Signiphoridae	75
		Eulophidae	3346
		Elasmidae	203
		Trichogrammatidae	630

Table 12.5. continued.

Hymenopteran families	Species described/ known	Hymenopteran families	Species described/ known
Rotoitidae	1	Vespoidea	
Mymaridae	1 303	Tiphiidae	1 500
Mymarommatidae	9	Mutillidae	3 500
Ichneumonoidea		Sapygidae	80
Ichneumonidae	15 000	Scoliidae	300
Braconidae	10 000	Bradynobaenidae	200
Chrysidoidea		Sierolomorphidae	10
Plumariidae	20	Rhopalosomatidae	33
Scolecbythidae	3	Formicidae	8 800
Sclerogibbidae	15–20	Pompilidae	2 000–3 000
Dryinidae	844	Vespidae	4 170
Embolemidae	12	Apoidea	
Bethylidae	1 000	Sphecidae	7 700
Chrysididae	3 000	Apidae	20 000
		Total	> 115 000

Sources: B. Bolton (pers. comm.), D.J. Brothers (pers. comm.), Brown (1982), J.M. Carpenter (pers. comm.), M. Day (pers. comm.), N. Fergusson (pers. comm.), I.D. Gauld (pers. comm.), Gauld and Bolton (1988), Kimsey and Bohart (1990), L. Masner (pers. comm.), Noyes (1990), Olmi (1984), D.R. Smith (pers. comm.), Townes (1969), Townes and Townes (1981).

The Total Described Fauna

To what extent can the spatial patterns of description of hymenopteran species in recent years be regarded as representative of those of all species of Hymenoptera described to date? The detailed distributions of species among countries is, of course, likely to be somewhat different. It seems probable, however, that the broad picture will be the same. If anything, it is reasonable to assume that although still comparatively small, the proportion of species of Hymenoptera being described from tropical regions is, when contrasted with earlier periods, quite high at present. Unlike groups such as the Lepidoptera and Coleoptera, assembling collections of tropical Hymenoptera was not a frequent colonial pastime, and the great collectors of the last century, such as Bates and Wallace, brought back relatively few specimens. Thus, the vast bulk of the 100 000–130 000 described species of Hymenoptera (Table 12.5; Southwood, 1978; Brown, 1982; Arnett, 1985) are of temperate origin. Estimates of the numbers of species known from a variety of regions tend to bear out this point (Table 12.6). The known North American and Australian faunas overlap very little in composi-

tion, and thus these two nations alone account for perhaps a quarter or more of described species of Hymenoptera.

Described Versus Undescribed

Quantification of the spatial patterns of species description in the Hymenoptera reveals clearly how drastically these differ from patterns in the actual levels of species richness. The magnitude of the gap between total numbers of species descriptions and faunal size in the various regions is, however, difficult to assess.

Table 12.6. The numbers of named or known species of Hymenoptera in various regions of the world, and the fraction these represent of all described Hymenoptera on the assumption that these number 100 000–130 000 species. The various estimates, including those for the global totals, were made at different times and are thus not strictly comparable. Note also that the regions are not all independent of one another, some are subsets of others.

	Species named/known	% of all described spp.
North America	17 429	13.4–17.4
Australia	14 781	11.4–14.8
British Isles	6 410	4.9–6.4
Canada	6 028	4.6–6.0
Japan	4 152	3.2–4.2
Israel	3 000	2.3–3.0
Norway	3 000	2.3–3.0
Philippines	2 446	1.9–2.4
Switzerland	2 300	1.8–2.3
Taiwan	2 000	1.5–2.0
Hawaii	651 (12 75*)	0.5–0.7 (1.0–1.3*)
New Zealand	549	0.4–0.5
Tasmania	546	0.4–0.5
Canary Islands	500	0.4–0.5
Barbados	365	0.3–0.4
Bermuda	199	0.2
Galapagos	62	<0.1
Cocos Is.	44	<0.1

Sources: Aagaard and Hagvar (1987), Bennett and Alam (1985), Chu (1989), CSIRO (1991), Danks (1979), Gapud (1984), Hilburn *et al.* (1990), Hogue and Miller (1981), Howarth (1990), A. Freidberg, (pers. comm.), Maa (1956), A. Machado (pers. comm.), Masner (1990), P.B. McQuillan (pers. comm.), Peck (1992), Sauter (1974), Stubbs (1982), and Valentine and Walker (1990).

*Including 624 aliens.

Table 12.7. The numbers of names species and the total numbers of species of Hymenoptera estimated for various regions.

	No. of species		Est. proportion named
	Named	Estimated total	
British Isles	5900	7220	0.82
Switzerland	2300	9000	0.26
North America	16500	32486	0.51
	17429	36000	0.48
Canada	6028	16665	0.36
Australia	7500	18166	0.41

Sources: Danks (1979), Masner (1990), Sauter (1974), and Taylor (1983).

Estimates of the proportions of species that have been named have, none the less, been made for the faunas of several temperate regions (Table 12.7; some of these figures differ from those in Table 12.6, this is because estimates of the numbers of described and undescribed species have only been used in Table 12.7 where they are from the same source). Though not all the remaining species in these cases will need to be described, as they will already have been described from other regions, these figures still serve to demonstrate that even in temperate zones the proportions of named species may be relatively low and their variation between regions great. Thus, although the bulk of present descriptive effort is directed towards temperate hymenopteran faunas, it remains insufficient to generate a complete understanding of the composition of one of these, for a reasonably sized area at least, in the immediate future. An optimistic estimate would suggest that probably more than 10% of the hymenopteran fauna of the British Isles is as yet unidentified, although this is frequently cited as having the best known fauna of any temperate nation with a moderate level of species richness. The present level of determinations of unnamed species in the British Isles is minimal.

Determinants of Descriptive Effort

What determines the present spatial distribution of descriptive effort? While a few nations are making concerted efforts towards getting their insect faunas described in their entirety (e.g. Australia, Costa Rica), for the majority, levels of description are determined in a much more haphazard fashion. They depend upon factors such as the numbers of taxonomists living in the country, the political stability of the country, its accessibility, the ease with which specimens can be transported in and out, whether major surveys have been carried out there, the history of taxonomic work upon the fauna and the availability of funds to pursue

Table 12.8. Estimates of the numbers of species described and the proportion these are of the numbers estimated to exist in families of Hymenoptera for Australia and for Canada. Data from Richardson (1983) and Danks (1979); higher taxonomy largely follows the former and differs from that preferred for Table 12.5.

	Australia		Canada	
	Named spp. ¹	Proportion ²	Named spp. ¹	Proportion ²
Xyelidae			2	5
Pamphiliidae			2	5
Argidae	2	5	2	5
Cimbicidae			1	5
Diprionidae			2	4
Tenthredinidae	1	5	4	5
Pergidae	3	5	1	4
Siricidae	1	5	2	5
Xiphydriidae	1	3	1	4
Orussidae	2	5	1	5
Cephidae			2	5
Trigonalyidae	2	5	1	5
Megalyridae	2	4		
Evaniidae	2	—	1	5
Aulacidae	2	—	2	5
Gasteruptiidae	3	—	2	5
Stephanidae	1	—	1	5
Ibaliidae	1	—	1	5
Liopteridae	1	—		
Figitidae	1	—	2	3
Cynipidae	3	—	3	3
Chalcididae	4	3	2	4
Eurytomidae	3	2	?	?
Torymidae	3	2	2	3
Aganidae	2	3		
Pteromalidae	4	2	3	3
Encyrtidae	4	2	3	3
Eulophidae	4	2	3	4
Trichogrammatidae	3	2	1	2
Mymaridae	3	2	2	2
Pelecinidae	1	1	1	5
Vanhorniidae			1	5
Roproniidae			1	5
Heloridae	2	5	1	5

Table 12.8. continued

	Australia		Canada	
	Named spp. ¹	Proportion ²	Named spp. ¹	Proportion ²
Austroserphidae	1	4		
Proctotrupidae	2	3	3	5
Diapriidae	3	2	3	4
Scelionidae	4	2	3	4
Platygasteridae	2	3	3	3
Ceraphronidae	3	3	3	3
Ichneumonidae	4	2	5	3
Braconidae	4	1	4	2
Loboscelidiidae	1	1		
Sclerogibbidae	1	—		
Dryinidae	3	—	2	4
Embolemyidae	1	—	1	4
Bethylidae	3	—	2	2
Chrysididae	2	3	2	5
Cleptidae	2	4	1	5
Tiphiidae	4	2	2	5
Mutillidae	3	—	2	5
Sapygidae			1	5
Scoliidae	2	4	1	5
Sierolomorphidae			1	5
Rhopalosomatidae	1	5	1	5
Formicidae	5	3	3	5
Pompilidae	3	—	3	5
Eumenidae	4	3		
Masaridae	2	5	3	5
Vespidae	2	5		
Sphecidae	4	3	4	4
Ampulicidae	2	—		
Collectidae	5	3	2	5
Halictidae	4	3	3	5
Andrenidae			4	5
Melittidae	1	5	1	4
Megachilidae	4	3	3	4
Anthrophoridae	4	4	3	4
Apidae	2	5	2	5

¹named spp.: 1 = 1–10, 2 = 11–50, 3 = 51–200, 4 = 201–1000, 5 = >1000²proportion: 1 = <10%, 2 = 10–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100%

further work. Few of these factors remain static. Moreover, a review of the patterns of descriptive work carried out over the careers of individual taxonomists reveals a strong opportunistic element. In many instances while the descriptive effort of such individuals is directed towards a particular group, there is no comprehensive attempt to describe the entire fauna of that group in one or more regions. Rather, descriptions are largely made of the species in collections which happen to come into the taxonomist's hands.

Where Next?

The determinants of the present spatial pattern of species descriptions are numerous, and their interactions complex. Unco-ordinated, their net effect has been to produce a body of species descriptions which provides an inadequate basis for determining much that we need to know about hymenopteran faunistics, both regionally and globally, and which continues to grow with disproportionate rapidity in regions of relatively low species richness. How this situation might best be altered is difficult to determine, and I would not presume to provide answers here. I would, however, make the following points.

1. Even in temperate regions work is too thinly spread to enable the documentation of the vast majority of species in any one region in the near future. In tropical regions, were *all* new descriptions to be made of species from one nation with a moderately rich fauna it would still probably take too long at current rates to gain a working knowledge of its species composition. This poses the question of where we should be asking funding agencies to apply their limited resources.
2. A substantial proportion of present descriptive efforts is consumed in the description of a few species from many nations for which few other species have been described. No funding agency would be content with such a dispersal of effort.
3. Most taxonomic effort seems to arise from serendipity not from any directed or managed attempt to elucidate particular problems. There will therefore be a conflict of interest between those who want to understand the overall patterns of, for example, species richness and distribution, and those who merely want to describe new taxa.
4. Attempting to develop a knowledge of entire regional hymenopteran faunas is probably an unattainable objective, because levels of description will not increase sufficiently. The best option would therefore seem to be to prioritize both the description of species from certain regions and from certain taxa. The proportions of species estimated to have been named vary both between families and between regions (Tables 12.8 and 12.9), making decisions as to how this prioritization is to be achieved yet more complex.

Table 12.9. The relationship between the numbers of named species and the proportion these are estimated to represent of all species for each of the hymenopter families in (a) Australia and (b) Canada. Data from Table 12.8.

Proportion named	Named species					
	1-10	11-50	51-200	201-1000	> 1000	
(a) Australia						
< 10%	2	—	—	1	—	3
10-25%	—	—	5	6	—	11
25-50%	1	4	1	5	2	13
50-75%	1	3	—	1	—	5
75-100%	4	7	1	—	—	12
(b) Canada						
< 10%	—	—	—	—	—	—
10-25%	1	2	—	1	—	4
25-50%	—	2	5	—	1	8
50-75%	4	3	5	1	—	13
75-100%	15	12	5	2	—	34

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What Does Tropical Society Want from the Taxonomist?

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Preamble

This chapter will mean different things to different people. Not all generalizations about the interface between systematics and the user apply equally to all taxa, to all institutions, to all regions of the world, to all subsets of taxonomists. My examples are meant to clarify a point and not to be an attack on the chosen example. It is a safe bet that I know next to nothing about the taxonomic status of your particular taxon or your own personal efforts to alleviate some of the problems mentioned here. If some of the attitudes or ideas expressed here are objectionable, instead of despairing, accept the challenge of coming up with a better solution to the general problem of what to do to ensure that we don't lose most of tropical biodiversity in the next five decades.

Introduction

The wording of the chapter heading is the message. I do not ask 'What does the taxonomist have to offer tropical society?' Tropical society's taxonomic needs recently have been, can be and should be a major rejuvenating force in systematics.

Tropical society wants, first and foremost, for the taxonomist to give it a cleaned up naming system, a cleaned up and workable set of Latin binominals and manipulation mechanisms for filing, comparing, searching, recording and working with the species-level units that constitute the backbone of the bountiful

biodiversity resource of tropical nations. Such a gift from the systematics community will give tropical societies the framework on which to hang and organize its biodiversity management, research, production, needs and aesthetics. Such a gift will position systematists quite centrally in the social explosion that is sweeping across the developing tropical nations.

In the majority of tropical countries the opportunity still exists to cause 5–20% of the national territory to become a conserved wildland that is highly valued, and therefore retained into perpetuity, for the diverse products of its wildland biodiversity. This means the retention and legitimization of 90% or more of the world's extant biodiversity. This means that we stop thinking about a country as divided into 'conserved wildlands' and 'production areas' and start thinking about a country as divided into two kinds of production zones, each with different products.

Placing conserved wildlands into sustainable and non-destructive production consists of three roughly consecutive steps. First, some wildlands need to be saved. This is most commonly manifested in a national park system. But one needs to know very little of taxonomic specifics to take this step. Second, you have to know what is in the conserved wildlands. This knowledge is not so as to protect them directly from poachers, fire, or ecotourists. This is so that society can know what is there, this is so that biologists and administrators can plan how to use their genes, chemistry, viewing populations and other products without destroying them. This is to produce an annotated catalogue for the warehouse and keep it well stocked. Third, you have to put wildland's products to work. This demands a biologically literate society and economy, a society and economy that can rely on the products from the conserved wildland.

Contemporary systematics is the language for the basic managerial, intellectual and scientific framework for non-destructive production from conserved wildlands. Without systematics, tropical conserved wildlands are little more than verdant countryside containing big trees, showy birds and woolly mammals, a biodiversity that humanity has handled with common names and lay concepts since time began. This may be all right in botanical gardens and zoos but it constitutes less than 1% of tropical biodiversity.

But – and this is a large but – systematics is like every other human guild. For more than two centuries, systematics has evolved its knowledge, technology and goals in response to a somewhat different set of social circumstances from those of a contemporary tropical developing society that recognizes the managed biodiverse wildland as one of its productive sectors. Here I examine a tropical national biodiversity inventory as something that a tropical society needs from the systematics community, the sorts of adjustments this need asks of systematists, and what this opportunity offers to systematics.

A National Biodiversity Inventory

Why go to the expense and effort to conduct a tropical national biodiversity inventory? Of what use is a list of species? Does it matter how many species are on the list or even whether they occur in that country?

It doesn't matter how many species are on the list; every tropical country with remaining wildlands of substance has hundreds of thousands of species. They will either become extinct or they won't. The importance of knowing whether they occur in the country is directly proportional to how much is known about them, rather than due to their presence in the list. The list of species is a by-product of an inventory – not the goal of the inventory. The list is the index in the shopping catalogue. The list is one of many ways to signal the existence and whereabouts of knowledge of what is in the greenhouse, the warehouse, the corporation's inventory.

So, when a tropical country asks for a inventory, it is not asking for a list of its species *per se*. It is asking for the building of a knowledge and reference system. For this system, a species list will appear as a by-product and index.

So, what is an inventory? At its minimum it is a taxonomically clean specimen and information data base that indicates at least one place in the country where a species can be found. As the country's biodiversity is studied and used by all walks of society, the inventory will come to be ever more rich in information on species' geographic ranges, habitat ranges and natural history (including references to whatever literature exists). The inventory will become taxonomically cleaner as a continent's biodiversity is studied and used by all walks of society. Other countries' inventories, new monographs, new biological information, cladistics, etc., will be the mechanics of this clean up.

What is the alternative to an inventory? As each species comes to be of interest or concern to someone in society, at that moment do whatever taxonomic and ecological homework seems to be necessary so that a lack of taxonomic or ecologic understanding does not impede action. We must be frank. Much of the interaction between extra-tropical society and biodiversity has been based on this principle. Much of the contemporary dwindling of interest in taxonomy in extra-tropical countries has its roots in this principle. But it is one thing when the biodiversity to manage is a single crop pest and two biological control agents, and quite another when the biodiversity is 300 000 species of insects being sampled for their defensive chemistry. And if the fate of a tropical country is to be one monomorphic agroscape, as is for example China, Haiti, Holland and El Salvador today, then a non-inventory methodology may be adequate (especially if it allows us to put more effort into the tropical countries that see something more interesting for their populace than rice fields, cotton fields and anthrodeserts).

National or Regional?

The actual unit of action for a tropical inventory may be anything from one country to a complex of countries that blanket some relatively natural geopolitical or biopolitical unit. Efforts such as those described here have the greatest chance of success if initiated under loving care and feeding by one country, but once established are quite likely to grow to encompass neighbouring countries and thus become regional by action rather than by political decree.

What Should Be the First Products of a National Inventory?

Identification guides for the species within a major taxon

When the systematists involved feel that they have better than 90% of the country's species in hand for a taxon, the taxon is ready for an identification guide. These should be compilations in formats appropriate to the in-country user community and to the ways that the guides would be used (field guide, laboratory guide, hard copy, CD-ROM, HyperCard stacks, etc.). The language should be that of the in-country user community, and it is highly desired that the guide be published simultaneously in English.

An identification guide should begin with a description and discussion of the natural history of the taxon, followed by a review of its overall degree of taxonomic cleanliness. Colour photographs of the species should be included wherever taxonomically useful, and drawings or black and white photographs otherwise. Each species should be represented by a block of information containing the following.

1. The most current Latin binominal, and common names if there are any; lacking common names, the Latin binominal becomes the common name as well.
2. Synonyms.
3. A brief taxonomic diagnosis depending heavily on reference to illustrations and stressing how to distinguish the species from other similar species in the guide.
4. A brief description of its overall geographic and habitat range as known to date.
5. A detailed description of its in-country geographic and habitat range as known to date, with localities tied to a thorough map and gazetteer of localities.
6. A detailed discussion of what is known of its biology overall.
7. A detailed discussion of what is known of its biology within the country.
8. Source (literature, field notes, etc.) for each factual block of information.

Traditional keys should receive minimal use, being replaced by pictorial keys and illustrations in almost all cases. Descriptions of new species should be published

in the traditional places for these, rather than in the identification guides.

Production – publication and other duplication processes – should be facilitated, if not completed, through desk-top publishing at the national biodiversity management institution. In-country publication is essential to ensure lowest prices and availability of the guides. Prices should be at cost. However, some of the information gathering may reasonably be viewed as part of the cost. On the other hand, it is also highly appropriate to subsidize the process as a way of maximizing the flow of the guides into the general populace.

Reference collections

The national reference collections, and their computerized associated specimen data, are the baseline working reference for the identification guides. These collections will also be used by later generations of taxonomists and biologists to verify identifications based on the identification guides, or sometimes to do the direct identifications. The reference collections are simultaneously the voucher specimens for the inventory locality data and for the identifications themselves. And even the identifications in the reference collection will shift somewhat as further studies reveal sibling species and polymorphic species that have been excessively lumped or split.

The specimens are also a massive data base for questions of intra- and inter-specific geographic variation in morphology, genetics, body chemistry, etc. Species and localities should be represented by long series, specimens that can be freely sacrificed in later years and centuries for chemistry, DNA and other uses unimagined today. While these specimens would not normally be in large enough numbers that they themselves could be of direct commercial value, research based on small samples of them could well be. The reference collections should not be confused with collections of vouchers for particular studies, vouchers that must be maintained to verify the names used in those studies.

The source of the national reference collections should be the collecting and sampling activities in the national inventory process. This process is carried out by parataxonomists and national curators, in collaboration with the international taxonomic community. The care of the reference collections, and their curatorial methodologies, should be state-of-the-art for the preservation of biological specimens into perpetuity.

Each species with a Latin binominal attached to it

Early in the inventory process it is commonplace to use codes for what appears to be species. However, by the time that an identification guide is published or otherwise made available there should be a formal Latin binominal attached to what is believed to be a species. Generic, tribal and subfamilial assignments may shift with time and greater analysis and knowledge, and synonymies will result in name changes, but experience has been that the user community can accommodate

to these formalized shifts far better than they can work with an ocean of species known by names such as 'the green shiny one with a red dot that sometimes eats trompillo' or '*Desmia* species 67'.

This part of taxonomic housecleaning will demand a lot of research papers with titles something like '47 new species of chrysomeline chrysomelids from Costa Rica'. These papers should be constructed, and their primary and secondary types distributed, with the thought in mind that their contained information will be used primarily to produce the national identification guides, aid in the later production of other identification guides for other tropical countries, and contribute to eventual monographs and cladistic analyses. For example, short descriptions and wide distribution of many paratypes may be much better than lengthy descriptions and micro-morphological studies done at the time. These descriptive papers should be in English, and thus maximally international in user-friendliness, rather than in the (perhaps other) language of the identification guides and their back-up data bases.

National administrative and technical staff

It is necessary to have a body of nationals who are philosophically and technically capable of biodiversity information management in an institutionalized administrative home that generates biodiversity products, uses these products, and generates more advanced inventory processes and products.

The national administrative and technical staff who conduct the national inventory – ranging from the parataxonomists to the curators to the directorate – constitute a nuclear human resource in the development and management of the nation's biodiversity resources. These persons have their roots in many different national and international traditions, but now form a novel institution that is neither museum, private collection nor government bureaucracy. It is a private, non-profit, public-interest node in the information flow from the nation's wildland living biodiversity to the final appreciators and consumers in-country and internationally.

As the national inventory nears completion, as well as long before this date to a lesser degree, this self-perpetuating cluster of human resources will find itself specializing in the gathering of biodiversity information – natural history, ecology, behaviour, etc. – directly from the nation's wildlands. Simultaneously, it will find itself immersed in the aggressive dissemination of this information, and associated samples, into the society-wide user community. This community can always use more awareness of what biodiversity products are potentially available.

The incorporation of the developed world's systematics community in the tropical development process

The international taxonomic community plays an extremely important role in

technical and philosophical guidance in the in-country formation of a national inventory. This is true technology transfer. But to do this, the international taxonomic community must abandon or diminish some of its own cherished taxonomic traditions and lifestyles, and put its abilities to work facilitating the process described here – a process that has much in common with the last two centuries of taxonomic work, but also differs significantly. Not all persons and institutions in the developed world will care to participate, but those that do will be an experienced body of ‘new taxonomists’ who will both have many decades of productive and appreciated opportunity ahead of them, and even, perhaps, be able to initiate some sort of similar process in their extra-tropical countries.

How Long Should it Take?

In a tropical country or small region where only 10–40% of the land is still wildlands, society has 10–15 years to demonstrate that its wildland biodiversity is a material and intellectual resource worthy of incorporation into the socio-economic fabric of the country. If the inventory is not complete and also well incorporated by then, the wildlands will probably be ploughed under by expanding population pressures and the disappearance of the economic inviability of tropical habitats, as biotechnology designs plants that can produce crops on what are viewed as the ‘worst’ soils and microlivestock that can eat virtually anything. In reply to the frequent comment that it is impossible to inventory several million species in a decade, my comment is that we either add in the resources and the mind-set to do it, or we kiss tropical biodiversity goodbye.

For those countries with less than about 10% of the land still remaining in (conservable or restorable) wildlands, it might well be best not to embark on the inventory process as outlined here, but rather to view the country’s few bits of remaining wildlands as national treasures to be restored and saved at almost any cost, a cost most likely to be paid by international connoisseurs of tropical biodiversity. Here, salvage collecting for living and dead gene banks may also be highly appropriate.

In those few cases where a tropical country still has more than 50% of its national terrain in wildlands, one can enter into the inventory process on a scale of several decades, or one can wait a decade and hope that (i) we can do a quicker and better job with those countries later through experiences gained today; (ii) the world might even evolve into a global level of understanding whereby such areas are conserved largely through the same forces that would today conserve 50 km² of English original forest, if there were any.

What is not an Inventory?

Ecological studies

Ecological, behavioural, etc., studies of the species being inventoried are, sadly, largely out of place in the inventory process. A kind of scientific triage is in order in these tight times. If ecological studies are to be funded and conducted, it should be where an explicit need in the biodiversity conservation process is being met and where the funds are clearly originating in that need (e.g. institutions funding ecological research, payback from commercialization of ecological information, etc.).

When mixed into an inventory, ecological sampling schemes almost invariably slow down the inventory process, and use funds that could have been used to speed or broaden the inventory. Once the identification guides are in hand, then the biodiversity package is available for all to work with – cladists, monographers, ecologists, ecotourists, school groups, biodiversity prospectors, etc. Ecotaxonomic sampling is a particularly difficult tradition to abandon in favour of inventory. Somehow it has become regal ‘to know what fraction of the fauna is present in a sample’. However, it is extremely difficult to identify where in the tropics such a sampling scheme is in fact needed for commercialization, straightforward conservation, education, etc.

To be blunt, a country does not want to know what fraction of the moth fauna comes to a black light. It wants to be able to identify the moths at the light so that it can begin to make a multitude of intellectual and commercial uses of them. This viewpoint is particularly difficult for ecologists, since they quite understandably want to apply their professional abilities to the general conservation problem at hand. Quite frankly, however, for the next several decades in the tropics, their energy could be better spent working on the multitude of ways that ecological understanding contributes to the flow of biodiversity information into the general populace and on specific ecological studies that enhance the non-destructive use of conserved wildlands by in-country society.

Cladistics

Establishing the phylogenetic relationships within the species-rich package of tropical biodiversity serves a very real organizational function. If these relationships are accurately established, the taxonomic framework is itself a highly functional tool in allowing the biologist to infer unknown traits of a species. And the more we get to know about certain species, the more effective is this tool. However, cladistic relationships are far easier to establish accurately in data-rich rather than in data-poor groups. This entire package of activity is definitely of second priority to the collection process and the identification guides. As with taxonomic monographs, cladistic analyses are far higher in quality when they contain the species-level input from several different national inventories.

Monographs

The systematist can work for decades, accumulating information throughout the range of some major taxon, and eventually publish a definitive monograph. This research style is, however, antithetical to a national inventory as envisioned here. It is far better to put several years of effort into establishing a detailed taxonomic and biological understanding of the focal taxon in several species-rich countries spread throughout the range of the focal taxon. These nodes of understanding will generate far more information overall about the focal taxon than the single taxonomic specialist could have gathered in several decades of work. With these processing centres in place, the taxonomist is in an excellent position to generate a final monograph. We might even begin to see multi-authored monographs, the product of real collegial activity between the international taxonomist and the specialist curators in the countries being inventoried.

PhD degree programmes

Put most simply, the developing tropical countries simply do not have the luxury of funds, time and human resources to bundle up their best people and send them off to spend decades in systematics PhD programmes in the extra-tropical countries. It must also be recognized that the PhD was a degree invented to meet a societal need and a university self-replacement need that does not fit particularly well in the developing tropics of today. We can all look forward to the day when a PhD in biodiversity information management or its analogue is a core portion of tropical developed society, but if we orient training today in that direction, there won't be any biodiversity information to manage in two decades.

How to Conduct a Tropical National Inventory

The national inventory process described here has two primary roots. The first, and very familiar to all international taxonomists, is the knowledge base in the minds, collections, literature and catalogues of the established international community of taxonomists. With a few exceptions in medicine and agriculture, this root has its primary origin in the search for taxonomic understanding *per se*. This search is on a nearly infinite time line and driven largely by the very great curiosity about biodiversity held by almost every international taxonomist. Not only does the international taxonomic community contribute to the national inventory process as mentor and with techno-philosophical guidance, but it can also contribute its very great information base and the gigantic taxonomic framework that it already has in place. It is this framework on which the Latin binomials and supra-generic names of a nation are hung.

Second, and more disruptive to the *status quo*, is a massive nation-wide collecting and specimen preparation effort carried out by national parataxonomists

and curators. They are trained for these purposes and hired from the appropriate sectors of society. It is they who bring in the actual specimens and get them into a format that leads to identification guides, reference collections, samples, etc. Again, the international taxonomist plays the role of mentor to apprentices, contributor to planning and sampling strategies, collaborator in the science and overall stimulant. His role needs to be primarily in-country and in the national language. When in his home institution, he is primarily a mentor to the apprentice in the specific processes of the inventory as well as doing taxonomy in collaboration with the national curators.

How Do Administrations in the Extra-tropical Systematics Community Become Involved and What Is the Cost?

The global mission

Administrations concern themselves with their institutional mission. This mission is traditionally defined by the society served by the institution. The first, the most difficult, and the most powerful step for an extra-tropical taxonomic institution or programme is to move from a provincial to a global outlook. The irony is that the large biodiversity institutions – national museums, large private museums, large universities, the USDA, CSIRO, IIE, etc. – have for more than a century been conducting a haphazard and opportunistic inventory of the tropics. But it has been focused and guided by the personal curiosity of staff or by the immediate economic concerns of the tax base, directions that change with the coming and going of individuals and the fickle fates of pest problems.

What is needed – desperately needed – is that these large administrations accept as a portion of their institutional missions a global responsibility for participation in the development of in-country biodiversity understanding in the tropics. This acceptance may be manifest either in facilitating their individual staff members to participate in the various focused national inventory efforts that are springing up across the tropics, and/or in guiding a portion of their institutional efforts in the direction of one or several of these national inventories. They can even help by being very public about their involvement.

On the one hand this acceptance will mean a material cost to the institution. Only the institution can evaluate to what degree it is compensated by the consequences – an increased global climate favouring the funding of biodiversity research, staff increase in morale through accepting a direct socially acceptable challenge, enormous multiplier effects in the form of nationals conducting their part of this extremely collaborative effort, long-term salvation of most of tropical biodiversity into perpetuity, etc. On the other hand, the bulk of the cost of tropical biodiversity inventory will be born initially by international development organizations and processes (as global capital investment), and by the tropical governments themselves. The annual operations costs will gradually be met by

the actual intellectual and economic gains from properly managed biodiversity information from conserved tropical wildlands. That is to say, no one expects that the world's established taxonomic institutions will bear the direct cost of tropical national biodiversity inventories.

And how much time can the extra-tropical institutions expect to have to participate in this kind of global process? Until the human war against tropical wildland biodiversity is over. This will be one to five decades, depending on the country. But I also suspect that by the end of this process the major biodiversity information management institutions will constitute a global network that will be the most intense in the tropics, and that today's strong balance towards extra-tropical institutions will no longer exist.

Convenios and agreements

When tropical taxonomy moves beyond being a collection of the activities of individual taxonomists, it is time for formal agreements of collaboration to begin to appear between the extra-tropical taxonomic institutions and the various national or small region inventory programmes. The most salient feature of such agreements is that they be written in such a manner that they facilitate the extra-tropical institution in its interactions with its funding base and in planning its long-range initiatives, and that they give the tropical country – justifiably nervous about its powerful northern neighbours – a proof and feeling that this is a truly collaborative effort.

Assigning taxonomists to such an effort

The interaction between the international taxonomist and the developing biodiversity inventory and its staff is sufficiently delicate that it is very important that all participants feel very content with their involvement. The adjustments are all very difficult in the best of times (learning new languages at middle-age, spending long times away from home without bringing back the specimens (booty) formerly associated with 'a trip to the tropics', co-authoring papers, sharing specimens, reduced rates of monographic publications, sharing one's lifetime memory bank of taxonomic information, living by others' schedules, formalizing one's work into something computerizable, etc.), and not something that can be easily assigned.

It has been the experience to date that making time and minimal resources available for those who want to participate is adequate to attract a sufficient number of international taxonomists to the tropical national biodiversity inventory process. An extra incentive is the case where an institution can assist with the costs of occasional working visits to the international taxonomist's home institution by nationals in apprenticeship or other forms of collaboration.

What Does the Taxonomist Have to Offer Tropical Society?

Tropical countries want taxonomists to join the teacher workforce that is putting biodiversity literacy into tropical intellectual and economic life. The taxonomist's alphabet, grammar and syntax offer us a far greater biological literacy than that ever held by our ancestors, who in their time had a quite elegant understanding of the wildlands in which they evolved. The contemporary taxonomist is not conscious of his fortune. When he walks through wildland nature, he can read it. Every insect is the title of a book. Every tree is a word in a paragraph. Every bird is a paragraph in a chapter. Humans can once again learn to read tropical wildland nature. Then it will no longer be a green oozy mass to be pummelled into the mud. Then it will be a cascade of books.

Hymenoptera?

And what does all this have to do with Hymenoptera? They are no exception.

Postscript

Even as I write this, my message is becoming obsolete. I believe that I am observing an extraordinarily rapid shift in attitudinal emphasis among taxonomists towards making their activity user-friendly. This shift is in fact quite amazing and impressive. The nature of taxonomic work is in itself highly conservative: it appears to select for practitioners with a proclivity for being slow to change – it doesn't.

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Measuring Biodiversity for Choosing Conservation Areas

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Introduction

Biodiversity has become a high priority for conservationists (e.g. Wilson, 1988; Reid and Miller, 1989; McNeely *et al.*, 1990; Reid *et al.*, 1992). This is a response to the widely held belief that many of the world's species may soon go extinct if the growing demand to exploit the remaining wilderness is allowed to act completely unchecked (Myers, 1979).

Priority areas must be selected for protection if we are to salvage the richest biodiversity, because not everything will be saved and wholesale biodiversity can only be conserved realistically *in situ*. But in order to know where most of the biodiversity is, we need to know how to measure it. Thus the precise definition of biodiversity could have far-reaching consequences.

What is meant by Biodiversity?

There are many possible definitions of biodiversity. McNeely *et al.* (1990: 17) define biological diversity rather broadly as an 'umbrella term for the degree of nature's variety, including both the number and frequency of ecosystems, species, or genes in a given assemblage'. Such a broad definition may satisfy most interests, but so far it has defied rigorous, practical measurement. In the past, the dominant tradition of diversity measurement has fallen short of this broad ideal by measuring diversity as species richness, such that all species are considered to be equal.

Ecologists have been particularly interested in understanding patterns in the composition of local assemblages of species. These patterns are seen as providing an insight into the ways in which resources are divided up among species. One approach to this study has involved diversity comparisons in which information on the evenness of abundance among species is combined with species richness (e.g. Peet, 1974; May, 1975; Southwood, 1978; Taylor, 1978; Magurran, 1988; Cousins, 1991). Yet some ecologists have recognized that the differing taxonomic relationships among species represent another important aspect of diversity (e.g. Pielou, 1975).

Conservationists have been concerned with maintaining faunas and floras, in addition to maintaining the utility and cultural value of the environment. Their interest has focused on preventing extinction, both locally and globally (e.g. Soulé, 1986). Therefore they have combined species richness with any population information that may be related to the perceived vulnerabilities of those species to extinction. This has included information on species' abundances, patchiness, endemism, restrictive ecological relationships and intra-population genetic variability (e.g. Usher, 1986). However, there has been a shift of emphasis from concern over the effects of habitat degradation on particular endangered species to the broader threat of mass extinctions (e.g. Myers, 1979). Consequently, conservationists have become more interested in the relative diversity within whole faunas and floras. In comparing diversity, they have called for greater value to be given to faunas and floras with species that are taxonomically particularly distinct (IUCN, UNEP and WWF, 1980: section 6).

The *Shorter Oxford English Dictionary* (1990: 585) gives a more general definition of diversity as meaning 'difference, unlikeness'. We have adopted a definition of biodiversity that includes not only the number of taxa in a sample, but also some measure of the *degree of difference* (in the sense of dissimilarity) among them (Vane-Wright *et al.*, cited in May, 1990; Vane-Wright *et al.*, 1991; Williams *et al.*, 1991). This assumes, using the social wasps of the Vespidae as an example, that a stenogastrine wasp and a hornet in Southeast Asia are more valuable for representing biodiversity than two species of *Vespula* yellow-jackets in Britain, because the Asian species are much more different from one another. Thus we concentrate on measuring present-day pattern and seek to minimize assumptions about possible diversification processes and possible future changes (cf. Anderson, 1974; Brooks *et al.*, 1992). To pursue this idea we need to be able to measure the degrees of difference between species.

Genealogical Difference and Branch Lengths

Clearly many kinds of differences could be recognized between species. We have attempted to measure the overall differences between species in terms of their genealogical relationships. This approach is based on the assumption that, in general, patterns of difference among species are most likely to be congruent with

the pattern of their genealogical relationships through genetic inheritance. Most systematists now accept that genealogical relationships are best inferred from classifications that have been constructed using cladistic methods (reviewed by Humphries, 1991; see also Nelson and Platnick, 1981; Wiley, 1981; Farris, 1983). Our measurements depend on describing the divergences between species in terms of their numbers of shared and unique nodes (branching points) within such a classification.

Our use of only the information in the pattern of nodes (branching points) in a cladistic classification may appear less quantitative than other measures that take into account the number of character state transformations detected along each internode (branch), such as genetic 'distance' (e.g. Altschul and Lipman, 1990; Crozier, in press) or morphological 'distance' (Faith, in press). Such branch-length estimates are often interpreted in terms of relative lengths of time (see Page, 1990). Unfortunately, this depends on two bold assumptions. Firstly, it must be assumed that the sensitivity of sampling for transformations in the sampled character set is unbiased among branches. Secondly, validity is assumed for the 'molecular clock' model (or its morphological equivalent) of effectively constant relative rates of transformation within character sets with time (e.g. Nei, 1987), at least as constant relative rates of transformation between sampled and unsampled character sets along different branches. However, we consider that sampling effects are likely to impose serious biases on these branch-length estimates, particularly in the case of morphological characters. We hope to reduce their effects by using information from just the branching order of the classification (some information of this kind can be gleaned from even existing classifications without time-consuming re-analysis). Of course, if the data from sampled characters were believed to be truly representative of overall differences among taxa, and if there were little or no homoplasy, then the cladogram could be redundant, because a dissimilarity matrix for those characters would be used directly by the pairwise diversity measures (Williams *et al.*, 1991).

In this chapter we review some of the kinds of difference in genealogy among species that can be used in cladistically based measures of biodiversity. Using these criteria, we seek to provide a basis for more appropriate and precise measurements of biodiversity for use in conservation.

Measuring Different Kinds of Taxonomic Diversity

Species richness (measure I)

If all species were regarded as being of equal value, then one of the simplest measures of diversity would be unweighted species richness, a count of the number of species present in an area. However, this is not to say that species are either easily defined as units (e.g. Otte and Endler, 1989) or that their number within an area is easily estimated (e.g. Palmer, 1990).

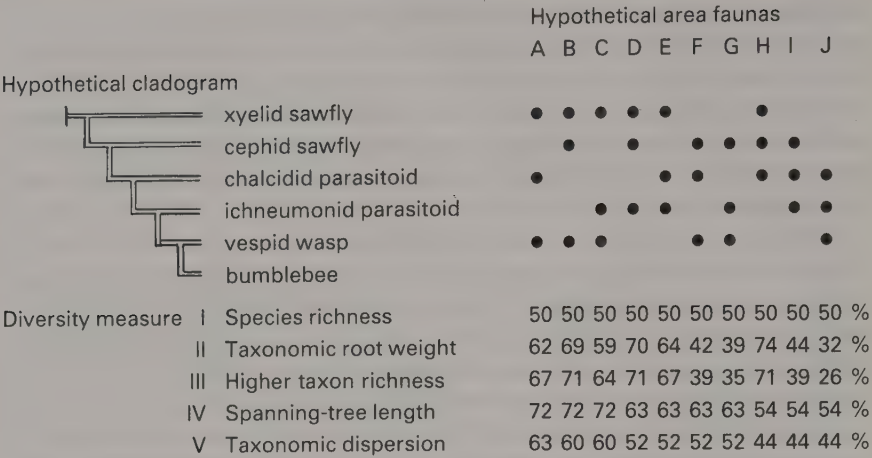


Fig. 14.1. Cladogram for the six surviving species of Hymenoptera after a hypothetical mass extinction. All ten possible faunas of just three species from among the first five are shown (this simplifies comparisons because the relationships of the last two species to each of the preceding species are the same for this cladogram, although note that faunas of three species with both of the last two species are not considered here). Diversity scores for faunas A–J using measures I–V are given as percentages of the total scores for all six species together. The cladogram is based on Gauld and Bolton (1988).

In order to discuss our interpretation of diversity, we consider a very simple case of a group of six species (Fig. 14.1). As a measure of diversity, species richness naturally lacks any discrimination of the degree of difference among faunas containing the same number of species (Fig. 14.1, measure I).

Real data often present unexpected problems, so we have also compared the properties of our diversity measures by applying them to a relatively simple example, the bumblebees of the *sibiricus*-group (Williams, 1991; Fig. 14.2). Conservation of bumblebees is not generally considered to be a high priority as yet, and the area units in Fig. 14.2 are too large to be realistic candidates for

Fig. 14.2. Current cladogram for the 43 species of bumblebees of the *sibiricus*-group in its broadest sense. The bold and fine unbroken lines on cladograms I–V are the subtrees showing the estimated relationships among the species of the highest-scoring faunas at the first and second step of a priority-areas analysis, using each of the diversity measures: I, species richness (Ecuador and Kashmir, India); II, root weight (Gansu, China, and Big Horn, USA); III, higher taxon richness (Baikal, USSR, and Kashmir); IV, spanning-subtree length (Gansu and Ecuador); V, dispersion (Gansu and Ecuador). For measure IV only the Gansu option for the first step fauna is shown because the other option, Kashmir, is similar (see the fine lines of the subtree for measure I).

protected area status. However, these data do show some of the problems. For instance, the most species-rich fauna is found in Ecuador, although this consists of closely related species that are descendants of just one, highly derived, subgroup (Fig. 14.2, measure I). This represents relatively little difference in genealogy among these species and so, in terms of our overall difference criterion, relatively little diversity.

'Close-to-root' species (measure II)

A second diversity criterion might be to attach particular value to the distinctive 'relic' species, such as the coelacanth, *Latimeria chalumnae*, among the vertebrates, or *Welwitschia mirabilis*, among the seed plants. These are the sole, taxonomically distinct survivors of long-independent lineages. To incorporate this criterion into diversity measures, it is necessary to find a way to search for faunas that have both many species and also particularly many of the species that diverged close to the root of the cladogram, with few surviving close relatives (Altschul and Lipman, 1990; Vane-Wright *et al.*, cited in May, 1990).

The taxonomic root weight measure weights species individually according to their genealogical distinctiveness, by measuring how close-to-root a species is in comparison to all of the species in a cladogram (Vane-Wright *et al.*, cited in May, 1990; Vane-Wright *et al.*, 1991; Williams *et al.*, 1991). The method proceeds by counting the number of nodes between the root of the cladogram and each species in turn. This count gives the lowest figure to the most valued, close-to-root species. In order to produce higher weights for the more close-to-root species, the total node count for the cladogram is divided by the node count for each species in turn. These individual species weights can be expressed as a percentage of the total node count for the cladogram and can be simply added together to give a faunal diversity score. Note that because species are weighted individually, a fauna with even a single species will receive a meaningful diversity score.

Figure 14.1 shows the success of the root-weighting method (measure II) in identifying fauna H as having the three most close-to-root species in the simple six-species case.

The ideas behind taxonomic weighting of species richness are shown very clearly using the bumblebees of the New World *fraternus*-group (a subgroup of the *sibiricus*-group). The map on the left in Fig. 14.3 shows the pattern of species richness, with its maximum in South America. The map in the centre of Fig. 14.3 shows the root weight score for each area divided by the number of species – this is the root weighting on its own, without species richness, and measures the average 'close-to-rootness' of the species in each fauna. It represents graphically the spatial pattern of the gradient from high-scoring faunas of early-diverging species in North America to low-scoring faunas of late-diverging species in South America that can be seen in the cladogram and table at the left of Fig. 14.3. The easiest interpretation of this kind of pattern to conceptualize is the

Bumblebees of the *fraternus*-group

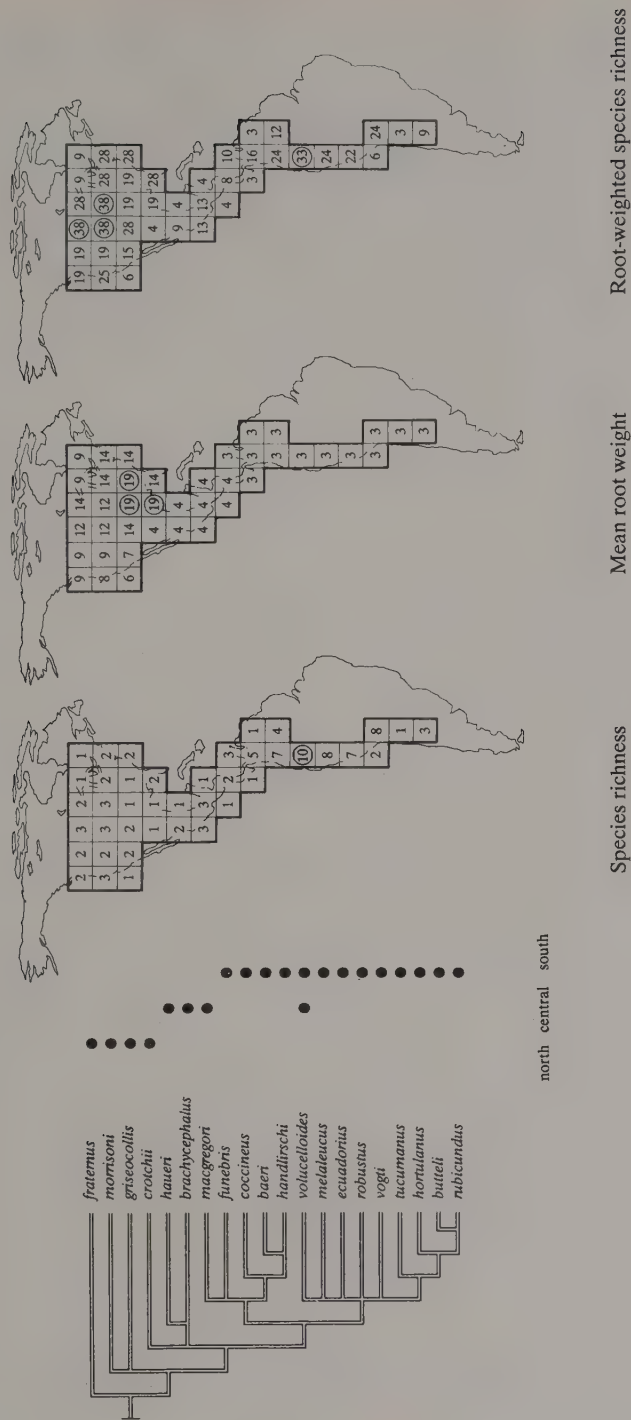


Fig. 14.3. Current distribution and diversity scores for the bumblebees of the *fraternus*-group (a New World subgroup of the *sibiricus*-group shown in Fig. 14.2). The figures for species richness are absolute numbers of species, although the root weight scores are given as percentages (fractions rounded down) on the sum of the root weights for the entire clade. For details of the equal-area grid, see Fig. 14.4.

dispersalists' 'Hennigian progression rule' (e.g. Brundin, 1988). This encapsulates the view that the most close-to-root taxa of a clade occur nearest to its 'centre of origin', whereas the most far-from-root taxa occur furthest away. From this perspective, it may be that the immediate ancestors of the *fraternus*-group reached the New World from Asia via Beringia, and then some of their descendants spread through corridors of suitable highland habitat from North America into South America within the last 3 million years (Williams, 1985). But for a taxonomic diversity score, the map on the right in Fig. 14.3 shows how the information on species richness and close-to-rootness can be combined in the root-weighted diversity scores, so that high diversity value emerges both for the few early-diverging species of North America, and also for the more numerous (though more closely related) species of South America.

When root weighting is applied to the entire *sibiricus*-group, the Gansu fauna shows the highest diversity score. This area has one species fewer (9) than Ecuador (10), the most species-rich area, but includes many of the most close-to-root species (e.g. *B. sibiricus*, *B. oberti* and *B. flaviventris*, Fig. 14.2, measure II). The highest incremental score is for Big Horn, USA, which adds in several more of the close-to-root species (notably *B. rufocinctus*).

Root weighting favours uniquely early-diverging species and not just any species that belong to different, higher taxa. For instance, in Fig. 14.1, fauna H receives a higher score by root weighting, measure II, even though it might be argued that any one of faunas B, D or H represents equal difference among the species in so far as any one of the chalcidid, ichneumonid or bee could represent the higher taxon Apocrita. This kind of value is implemented in measure III, higher taxon richness.

A serious problem for root weighting arises from the present method of calculation if cladograms are not fully resolved (due to lack of information), because the node counts for some of the unresolved species will then be artificially low. May (1990) suggested a modification of the root weight measure that appears to reduce this problem by taking into account the number of branches at each node. However, if we were seeking higher taxon richness as a criterion of diversity, May's modified measure would actually give a less desirable answer (Williams *et al.*, 1991). Because the modified measure increases the weight of a pair of sister species relative to an unresolved 'bush' of species at the same number of nodes from the root, a fauna consisting of the two sister species would score more highly than a fauna with one of the sister species and one from the other group with the bush of species. Consequently, this result is the opposite of what is required from a measure of higher taxon richness.

Higher taxon richness (measure III)

An obvious progression from root weighting for close-to-root species is to value higher taxon diversity, irrespective of the total number of surviving species in each higher taxon. To incorporate this criterion into diversity measures, we must

find a way to search for faunas that have many species and also are representatives of as many higher taxa as possible (Williams *et al.*, 1991).

One way of measuring the number of higher taxa in a fauna is to use pairwise measures of cladistic divergence between species. For a fauna in which more of the higher taxa are represented, the species will tend to diverge closer to the root of the cladogram. Consequently, the species will have a lower average number of shared nodes from the root of the cladogram. Therefore we can measure the higher taxon diversity of a fauna by the product of its species richness with the mean inverse number of shared nodes from the root of the cladogram (i.e. number of spp \times mean $1/S_{ij}$, for all pairwise comparisons between species *i* and *j*, Williams *et al.*, 1991). Note that because species are weighted from pairwise comparisons, only faunas with at least two species will receive a meaningful diversity score (for our computer implementation of these measures, faunas with single species are given an arbitrary score of zero, although their presence is still registered on the map). As before, faunal scores can be expressed as a percentage of the total diversity score for a cladogram. However, unlike root weight scores, the faunal scores by higher taxon richness are no longer simply additive, because the cumulative score must take into account the cross comparisons between those species not shared by the separate faunas. So the diversity increment when one fauna is added to another is calculated as the difference between the score for the pooled fauna and the score for the original fauna.

The success of this pairwise measure for higher taxon richness in identifying the fauna with the three highest taxa in the simple six-species case can be seen in Fig. 14.1 (measure III, giving faunas B, D and H equal scores because they include the xyelid, the cephid and one representative of the Apocrita).

When higher taxon richness weighting is applied to real data for the *sibiricus*-group, the Baikal fauna has the highest diversity score. This area has half the number of species (5) of Ecuador (10), the most species-rich area, but includes three of the four highest-ranking taxa (Fig. 14.2, measure III; no fauna has all four of the highest taxa). The highest incremental score is for Kashmir, which adds several more of the remaining highest taxa within these groups.

Although the highest-ranking taxa of the *sibiricus*-group are well represented by these two faunal choices, the variety of subgroups is not well represented because of the strongly asymmetric topology of this classification. Consider the six Hymenoptera in Fig. 14.1. A higher score would be given to a fauna with the xyelid sawfly, the cephid sawfly and the chalcidid parasitoid (Fig. 14.1, fauna H favoured by higher taxon richness, measure III), than would be given to a fauna with the xyelid sawfly the chalcidid parasitoid and the vespid wasp (Fig. 14.1, fauna A favoured by taxonomic dispersion, measure V described below). Consequently, some measure of the variety of subgroups within the cladogram is needed.

Spanning-subtree length (measure IV)

In seeking to measure diversity as the variety among organisms, another simple criterion is to measure how much of the cladogram is represented by a fauna. To incorporate this criterion into diversity measures, we must find a way to search for faunas that have many species and also species representing a particularly large proportion of the overall amount of cladistic divergence.

The measure of spanning-subtree length (or cladistic 'path' length) used here measures the genealogical divergence among a fauna by adding up the number of intervening nodes on the cladogram between all of the species included in the fauna, counting each node only once (this can be similar in effect to pairwise measure iv in Williams *et al.*, 1991). It counts each species as an additional terminal node, but does not include any nodes between the root of the cladogram and the most basal node of the spanning subtree itself. Note that because species are weighted from numbers of nodes between species, only faunas with at least two species will receive a meaningful diversity score (just as for higher taxon richness, faunas with single species are given an arbitrary score of zero, though their presence is still registered on the map). Faunal scores can be expressed as a percentage of the total diversity score for a cladogram. Like higher taxon richness scores, the faunal scores by spanning-subtree length are not simply additive, because the cumulative score must increase by only those nodes between the new species and the previous spanning subtree. So the diversity increment when one fauna is added to another is calculated as the difference between the score for the pooled fauna and the score for the original fauna.

The success of this spanning-subtree length measure in identifying the fauna with the three most divergent species in the simple six-species case can be seen in Fig. 14.1 (measure IV, giving faunas A, B and C equal scores because they include the xyelid, the vespid wasp and any one from among the cephid, chalcid and ichneumonid).

When spanning-subtree length weighting is applied to the *sibiricus*-group, the faunas with the highest diversity score are Kashmir and Gansu. Each of these areas has fewer species (9) than Ecuador (10), the most species-rich area, but they include two, rather than one, of the four highest taxa (Fig. 14.2, measure IV). The highest incremental score is for Ecuador, which adds a large sample of the divergent and species-rich South American taxa.

This measure of spanning-subtree length shows relatively poor discrimination between faunas with differing taxonomic relationships among the species. For instance, the six-species case in Fig. 14.1 gives only three levels of diversity score, which is the lowest for any measure here other than unweighted species richness. In particular, it fails to ensure that those faunas with species that are more evenly distributed across the cladogram score more highly (Fig. 14.1: fauna A receives the same score as faunas B and C).

Taxonomic dispersion (measure V)

A refinement of spanning-subtree length is to value faunas that represent the variety of subgroups in a cladogram most evenly. To incorporate this dispersion criterion into a diversity measure, it is necessary to find a way to search for faunas that: (i) have many species; (ii) have species that are cladistically very divergent; and (iii) have species that are most evenly spread across the subgroups of the cladogram (Williams *et al.*, 1991).

Taxonomic evenness can be measured using the relationship between the mean and the standard deviation of pairwise divergences among species. An appropriate measure of genealogical divergence is provided by a simple count of the number of nodes on the cladogram between two species (i.e. $U_{ij} + U_{ji} + 1$, the sum of the nodes unique to species *i* in relation to species *j*, and unique to *j* in relation to *i*, plus one), because information on the position of the root is not needed for evenness. For a fauna with species that are distantly and evenly spread across a classification (i.e. highly dispersed), the average divergence among the species will be high and the distribution of divergences around this average will be narrow.

Williams *et al.* (1991) proposed a first, crude measure of taxonomic dispersion that is given by the product of species richness and the difference between the mean pairwise divergence and the standard deviation of those pairwise divergences: i.e.

$$\text{number of spp.} \times [\text{mean divergence } \{U_{ij} + U_{ji} + 1\} - \text{s.d. of divergences } \{U_{ij} + U_{ji} + 1\}]$$

for all pairwise divergences within a fauna. However, they realized that this particular implementation of the dispersion criterion has some undesirable properties. For example, in some circumstances *adding* a species to a fauna can reduce the evenness of the representation of subgroups sufficiently for this measure to actually yield a *reduced* diversity score (i.e. it is not a monotonically increasing function of species richness).

Here we measure taxonomic dispersion using the product of species richness with the sum of the mean pairwise divergence and the ratio of the mean pairwise divergence to the standard deviation of those pairwise divergences plus one:

$$\text{number of spp.} \times [\text{mean } \{U_{ij} + U_{ji} + 1\} + (\text{mean } \{U_{ij} + U_{ji} + 1\}) / (1 + \text{s.d. } \{U_{ij} + U_{ji} + 1\})]$$

for all pairwise divergences within a fauna. This overcomes many of the problems with the previous implementation. Note that because species are weighted from the evenness of pairwise comparisons, only faunas with at least three species will receive a meaningful diversity score (faunas of one or two species are given an arbitrary score of zero, although their presence is still registered on the map). Faunal scores can be expressed as a percentage of the total diversity score for a cladogram. However, as for the higher taxon richness scores, the faunal scores by dispersion are not simply additive, because the cumulative score must take into

account the cross comparisons between those species not shared by the separate faunas. So the diversity increment, when one fauna is added to another, is calculated as the difference between the score for the pooled fauna and the score for the original fauna.

Figure 14.1 shows the success of this taxonomic dispersion measure (measure V) in identifying fauna A as having the three most evenly and strongly divergent species in the simple six-species case.

When the new dispersion weighting is applied to the *sibiricus*-group, the Gansu fauna has the highest diversity score. This area has fewer species (9) than Ecuador (10), the most species-rich area, but it includes two rather than one of the four highest taxa (Fig. 14.2, measure V). The highest incremental score is for Ecuador, which adds species from the most divergent and species-rich South American taxa.

Although the subgroups of the *sibiricus*-group are more evenly represented by these two faunal choices, because of the asymmetry of the cladogram the higher taxa cannot at the same time be as well represented as might be the case with the higher taxon richness choices (measure III). Consider the six Hymenoptera in Fig. 14.1. A higher score would be given to a fauna with the xyelid sawfly, chalcidid parasitoid and vespid wasp (Fig. 14.1, fauna A favoured by taxonomic dispersion, measure V), than would be given to a fauna with the xyelid sawfly, cephid sawfly and chalcidid parasitoid (Fig. 14.1, fauna H favoured by higher taxon richness, measure III).

Which Kind of Biodiversity do we want to Conserve?

If we accept that diversity includes a concept of degree of difference among species, not only must we decide which attributes of species it is practical to compare, but also we must decide which kinds of difference are important. Furthermore, no single measure can give the 'best' answer in every situation, because all weighted measures must be a compromise between species richness and degree of difference (Williams, *et al.*, 1991). In practice, the kind of difference that is valued often changes with the context. Clearly, it would help if biologists could agree on which measure is closest to the single most widely held concept of biodiversity.

Our results with very simple data (Fig. 14.1) show that fundamental distinctions exist between some of the kinds of difference that are likely to be important in biodiversity, particularly between the concepts of higher taxon richness and taxonomic dispersion. The measures of taxonomic root weight and higher taxon richness follow a more strictly cladistic philosophy, in so far as they explicitly use polarity from the root of the cladogram to weight higher ranking taxa at the successive divergences of lineage. In contrast, spanning-subtree length and taxonomic dispersion are more general tree measures of subtree 'representativeness', to which the root of the cladogram contributes no more than a node between the

highest ranking taxa, so that polarity is ignored at this stage of the analysis.

This dichotomy is significant because it raises the question of whether the 'difference' in the definition of diversity (see the Introduction) should be taken literally as the obverse of similarity in the simple phenetic sense, or whether the special cladistic sense of derived or less general similarity is required within the diversity measures themselves. We have argued for the study of the cladistic patterns in sampled character sets for the inference of genealogical patterns, but then for these patterns to be used to infer the overall genetic and phenetic differences, in the belief that unrestricted differences are the currency of biodiversity in the popular conception. Diversity measures still need to be based on cladistic, genealogical classifications in order to minimize the bias that results from gene and character sampling (see the Introduction). Our results with simple test data show that, of the diversity measures that go on to use unrestricted genealogical differences (Fig. 14.1, measures IV and V), taxonomic dispersion appears to be closest to seeking out the pattern of difference valued in the popular concept of diversity. Thus our present preference among all of the diversity measures described here (and among others in Williams *et al.*, 1991) is for taxonomic dispersion. Spanning-subtree length may also be useful, even though it does not measure evenness and is less discriminating among different taxonomic relationships, because it provides a crude measure of subtree representativeness that is easier to calculate.

Priority-areas Analysis for Conservation

Cost effectiveness from complementarity

Biodiversity measurement is not technological overkill, but absolutely essential, if conservationists are serious about biodiversity *per se*. It may be apparent where the single greatest biodiversity 'hot spot' is situated (Myers, 1988, 1990), particularly when specialists have only to identify a single hot spot for a restricted taxonomic group. It may even be possible to identify a major centre of overall diversity using correlated environmental variables (e.g. actual or potential evapotranspiration, for the terrestrial environment, see Currie, 1991). But the difficulty arises when priority choices are needed from among the remaining areas once the initial hot spot has been identified (e.g. IUCN and WWF, 1987; Prance, 1990). Therefore in order to make cost-effective networks of protected areas (Margules and Austin, 1991), we need to know how to maximize the amount of biodiversity that can be captured, both from suboptimal choices, and also with the second and successive choices. This more precise prioritization requires taxonomic inventories, diversity measures and complementarity (Vane-Wright *et al.*, 1991).

The complementary part of a fauna is just those species that are not represented in another fauna with which it is being compared. For instance, in our

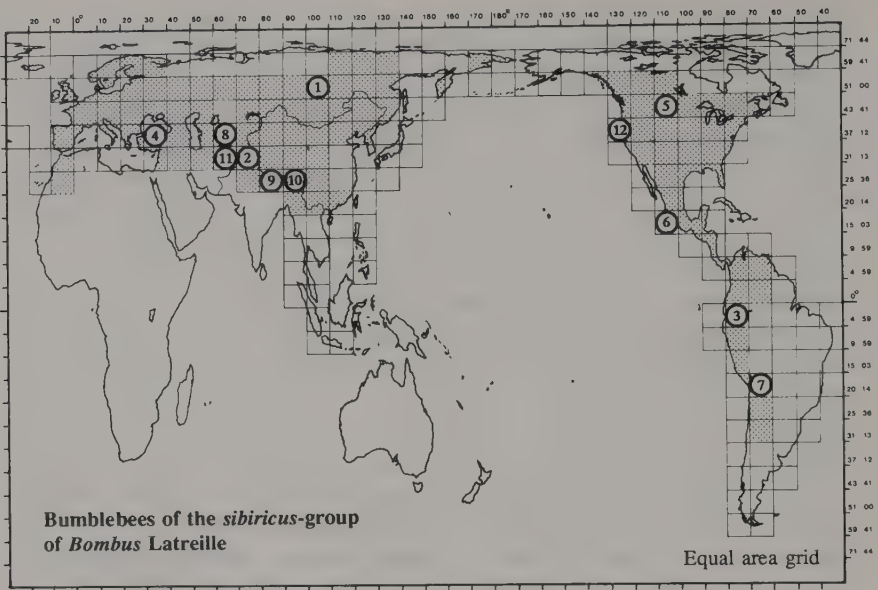


Fig. 14.4. Example of a crude, global priority-areas analysis for the bumblebees of the *sibiricus*-group. The optimal sequence of area choices by species richness weighted by higher taxon richness (scores are plotted in Fig. 14.5) is shown by numbers in the grid-squares: 1, Baikal (former USSR); 2, Kashmir (India); 3, Ecuador; 4, Turkey; 5, Big Horn (USA); 6, Michoacan (Mexico); 7, central Bolivia; 8, Samarkand (former USSR); 9, Nepal; 10, Arunachal Pradesh (India); 11, Hindu Kush (Afghanistan); 12, northern California (USA). The map is based on a cylindrical, equal-area projection, orthomorphic at 45° N/S (where bumblebee records are particularly numerous). The grid is calculated from intervals of 10° longitude to provide equal sampling areas, which appear as squares on this projection. The portion of the grid shown (251 squares) covers the known, native distribution of all bumblebees (c. 250 species). The shaded land area lies within the 121 grid-squares from which the bumblebees of the *sibiricus*-group are known.

stepwise priority-areas analysis, once a first high-diversity fauna has been chosen, the second priority fauna is selected by virtue of its high incremental diversity score based solely on consideration of the faunal complement. Once the second choice has been established, the third choice is based on considering the complement of the first two, and so on, until the complement is reduced to zero (i.e. all species have been represented at least once). This idea of complementarity is not new, but its potential has not always been recognized and it deserves emphasis. It is fundamental to our priority-areas analysis and to the method of Kirkpatrick (1983), to Critical Faunas Analysis (Ackery and Vane-Wright, 1984), to Network Analysis (e.g. Margules *et al.*, 1988) and to Gap Analysis (Bruce Stein, pers. comm.)

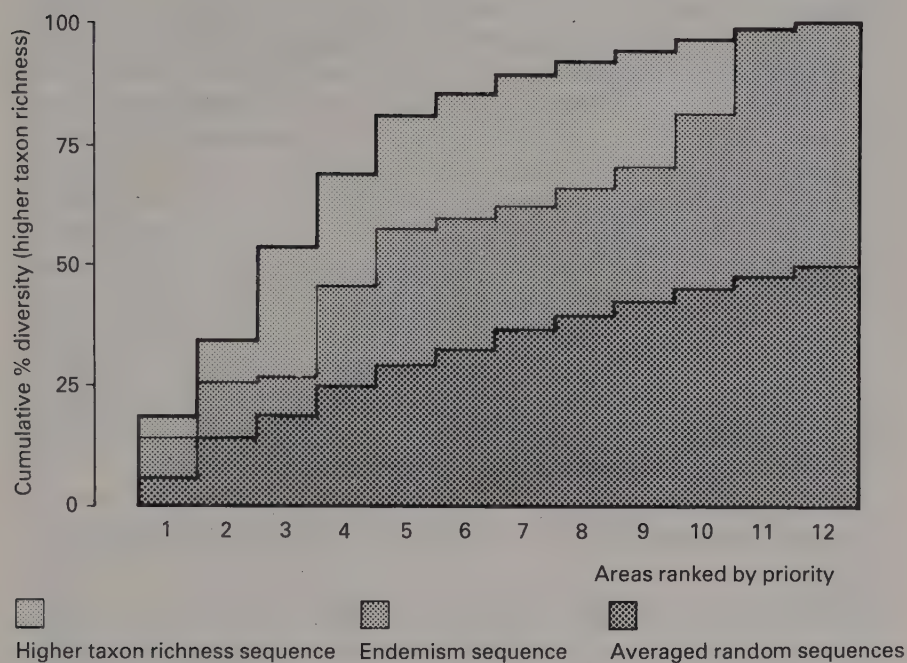
Priority-areas analysis: bumblebees of the *sibiricus*-group

Fig. 14.5. Superimposed histograms of biodiversity scores from three methods of priority-areas analysis when choosing faunas of bumblebees of the *sibiricus*-group. Diversity is scored for this example using species richness weighted by the higher taxon richness of the cumulative fauna at successive steps. Faunas are chosen: upper line, to maximize the higher taxon diversity score (this sequence of areas is mapped in Fig. 14.4); middle line, to maximize the number of narrowly distributed (endemic) species, using maximal species richness among tied scores; and lower line, by random draws, using the average scores from 1000 simulated sequences.

Priority-areas analysis provides a means of choosing sequences of areas in an order that represents their priority for the conservation of biodiversity. For example, using the bumblebees of the *sibiricus*-group with diversity measured as higher taxon richness (Figs 14.4 and 14.5), a priority-areas analysis for maximizing diversity performs very much better in accounting for their diversity (Fig. 14.5) than either selection by chance, or the kind of selection by endemism and species richness that is often used in conservation (Vane-Wright, in prep.). Priority-areas analysis is also flexible enough to take account of any existing protected areas, if required. The method is now being appraised in IUCN Species Survival Commission conservation projects for milkweed butterflies (Danainae)

and fruit bats (Pteropodidae) world-wide, and for Afrotropical antelopes (Bovidae).

With the introduction of faunal complementarity, conservation evaluation strictly for taxonomic diversity may no longer require a preliminary habitat classification. This has been used previously because it was argued that ecological, abundance-based diversity measures are only of use for assessing conservation priorities when they are applied to comparisons of similar habitats (e.g. Magurran, 1988). Different habitats can now be compared more directly, which removes the problem of the need to impose a classification with an arbitrary number of habitat 'types' onto the complex variation of natural species assemblages (cf. debate concerning the classification versus ordination approaches to the description of vegetation, e.g. reviews in Shimwell, 1971; Greig-Smith, 1983). For example, if the most taxonomically diverse assemblage of species on land were indeed in an area of tropical wet forest (e.g. Myers, 1988), then it would have the highest diversity score. But even very different kinds of habitat, perhaps with many fewer species, should come high on the list of priorities if those species that they do have are complementary and genealogically very divergent.

Geographical information systems: rationality and flexibility with conflicting land use values

In practice, priority areas for conservation usually have to be chosen with regard to many conflicting values, of which biodiversity is just one (e.g. Usher, 1986; ODA, 1991; Reid *et al.*, 1992). Consequently decision-makers need to weigh evidence from large quantities of data. The tasks involved are often time-consuming and repetitive, which makes them ideal candidates for automation using computers. Manipulating data on the distribution of biodiversity is a geographic information system (GIS) problem (Scott *et al.*, 1987). These computer aids can manage data bases for any biological, political, economic or other values related to land use that can be measured, and they are particularly effective for the visual communication of any spatial pattern in these values (e.g. Burrough, 1986). For example, GIS could apply filters to select data from the data base at a scale appropriate for a particular planning project. The biological, economic and other values for areas could then be displayed in various combinations as map overlays on the computer screen. It is essential that all of these values are made explicit and rational, and not hidden in general, subjective judgements (Morowitz, 1991). For prioritizing protected areas for conservation, GIS together with our interactive methods could give decision-makers the flexibility and speed to assess more of the available options at each step, while taking into account not only biodiversity scores as described here, but also the many other competing interests.

The biodiversity measures described in this chapter could be implemented as a GIS tool to produce scores for areas at *any* spatial scale. We are also exploring

whether our measures can be applied at higher taxonomic levels to compare diversity among entire faunas and floras for the kinds of general survey that are now being proposed (e.g. Solbrig, 1991a, b; Reid *et al.*, 1992). This might entail some loss of cladistic rigour when using some current classifications, and would face the perennial problem of parity of status among higher taxa of the same nominal rank, but it does represent a more direct approach to the problem of measuring wholesale biodiversity.

Conclusions

1. We recognize that a fundamental part of the concept of biodiversity is the variation in degree of difference among organisms.
2. General differences among organisms can be measured using information from genealogical classifications.
3. Conflicting kinds of difference in genealogy can be recognized, such as higher taxon richness and taxonomic dispersion. The latter may be closer to a popular idea of a measure of biodiversity. Further trials of these measures are needed.
4. Once a measure of biodiversity can be agreed, faunal complementarity can be used to prioritize potential protected areas for cost-effective conservation of the maximum or optimum amount of biodiversity.
5. The selection of areas for protection could soon be based on more rigorous, rational methods that should give repeatable results when applied by different conservation analysts.

Summary

One of the major goals of conservation is the maintenance of as much of the diversity of life as possible. Clearly if we are to be able to choose between areas in order to be able to protect the greatest overall amount of biodiversity, then we will need to be able to measure and compare local biodiversity. This has generally been measured only in terms of species richness, or by using indices that combine species richness with information on relative abundance. Such measures are considered unsuitable for the task in hand. Diversity is considered here to include a concept of difference, and the most generally appropriate measure of this difference is likely to be made in terms of the genealogical relationships between species. We review various taxonomic measures of faunal diversity that can be used to prioritize local areas within a global or regional context. By employing faunal complementarity, stepwise procedures can then identify optimal sequences of priority areas for protection, taking existing protected areas into account or not, as required. These methods are illustrated by their application to examples from the Hymenoptera.

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Costa Rica: an Innovative Approach to the Study of Tropical Biodiversity

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Introduction

There is widespread agreement that environmental degradation and the consequent loss of species is one of the major problems confronting humanity today (Grosvenor, 1988; Wilson, 1988; Anonymous, 1989a, b; Chalker, 1991; WRI, IUCN, UNEP, 1992). However, most terrestrial biodiversity occurs in tropical countries, and many of these are the nations that can least afford to conserve natural resources (Smith, 1990). They are beset by the burdens of a chronic economic crisis, crippling national debts and a rapidly expanding population (Simons, 1988; Ramphal, 1989). Increasingly, many are having to use their natural assets for short-term gain, and most simply must make economic use of their wildlands.

The Costa Rican Situation

For Costa Rica, a small but remarkably biologically diverse country in Central America (Janzen, 1983), this was a particularly challenging problem as the nation has one of the world's most progressive conservation policies. After two decades of conservation effort Costa Rica has established about 12000 km² of conservation areas, land that comprises nearly 25% of its territory. This system is thought to protect about 500 000 species of animals and plants, perhaps 5% of the total terrestrial biodiversity of this planet (Gámez, 1991; Janzen, 1991). The Costa Rican government realized the social difficulties that would be encountered

by trying to preserve reserves of such size, and decided they could only be maintained permanently if they were integrated economically and intellectually into the society that owns them. They will only survive if the Costa Rican people value and appreciate them. Thus in 1989 the government recommended the establishment of a private, non-profit-making, public interest organization for the purpose of 'putting biodiversity to work for society'.

The Creation of INBio and its Objectives

The National Biodiversity Institute (Instituto Nacional de Biodiversidad: INBio) was thus established to promote the conservation of biodiversity through facilitation of its sustainable use by Costa Rican society. This goal was deemed to be attainable by conducting three sequential and somewhat overlapping steps: saving biodiversity, knowing it and putting it to use (Gámez, 1991; Janzen, 1991). The first has largely been completed in Costa Rica, but the objectives of INBio are to bring about these vital second and third steps. INBio strives to involve in this effort widely different sectors of Costa Rican society, with the clear understanding that substantial financial and intellectual support is required from the developed world.

Getting to Know Biodiversity

Before biodiversity can be put to use it is necessary to know what there is that has been conserved, that is, there is a need for a biotic inventory. INBio aims to conduct a ten-year total biodiversity inventory of Costa Rica in order to know what species exist in its wildlands and where these are, and to disseminate this information to society in an easily accessible form. As can be imagined, such an inventory requires the collection and taxonomic organization of a vast amount of information. If this process were to be undertaken following the traditions of the academic scientific community, then it would require time and human and economic resources simply not available to a small tropical country. In consequence an entirely new approach had to be developed, using local human resources – people specifically trained with this goal in mind.

One group of these people, former park guards and lay persons from rural backgrounds, have become INBio's army of 'parataxonomists'. They have received a vocationally oriented practical course in basic biology, ecology and taxonomy, collection and preparation of biological specimens, and the fundamentals of administration required for an individual to understand and conduct a specific portion of a biodiversity inventory. Thirty-one parataxonomists have been trained in two courses between 1989 and 1990 and currently, in 1992, a further group of 21 are undergoing training (Janzen and Hallwachs, 1992) When

trained the parataxonomists work full time, with little supervision in one of the 19 biodiversity offices located in the various conservation areas throughout the country. The biological material and information they collect are analysed, processed and discussed with them when they come to INBio headquarters in their periodic monthly visits.

Parataxonomists perceive their new job as an intellectual promotion and become agents of the social extension of their work into their own communities and parks, where they rapidly start disseminating their knowledge among relatives, neighbours and local schools (Janzen, 1991).

The biological specimens and information collected by the parataxonomists flow to the INBio headquarters where experienced and apprentice local curators initiate the taxonomic organization of the material (see Fig. 15.1). Specimens are identified as far as is possible, depending upon individual experience and available literature about the particular taxonomic group. Like that of a parataxonomist, the apprentice curator is a new kind of job specifically created to address the needs of the inventory and the biodiversity crisis as a whole. These curators are young men and women graduates with a strong desire to study a particular group of organisms. They receive practical on-the-job training from more experienced colleagues, and interact closely with visiting international taxonomists. Several have received grants enabling them to study for periods in major museums in the United Kingdom or the United States (Gómez, 1991; Janzen, 1991).

INBio has actively sought the collaboration of the international biosystematics community, and many taxonomists have worked at INBio on a particular group of organisms in direct collaboration with the local curator. This type of partnership has accelerated the identification of the specimens and contributes directly to the development of Costa Rica's capacity to undertake its biological inventory.

The implementation of the parataxonomist programme and the partnerships of Costa Rican and international biologists described above have allowed the development in 36 months of a properly organized insect collection with over 2 million specimens. By comparison, during the previous 110 years only about 50 000–80 000 specimens had accrued in national collections. The value and range of collections assembled by INBio and its collaborators can perhaps most strikingly be appreciated in the context of a recent taxonomic revision of pimpline ichneumonids (Gauld, 1991). The original national collection of Costa Rican insects stored in the Museo Nacional included eight species; the major world class institutions – including The Natural History Museum in London, the US National Museum and the American Entomological Institute in Gainesville – had between them an additional 37 or so species from Costa Rica. The revision recognized 161 species, most of which have only been collected as part of the current intensive biological survey of Costa Rica. Thus these biotic surveys increased the known fauna of one small group of ichneumonids more than three-fold, and provided a firm basis for a substantial taxonomic monograph relevant

National Biodiversity Institute of Costa Rica (INBio)

Inventory flow from field to public use

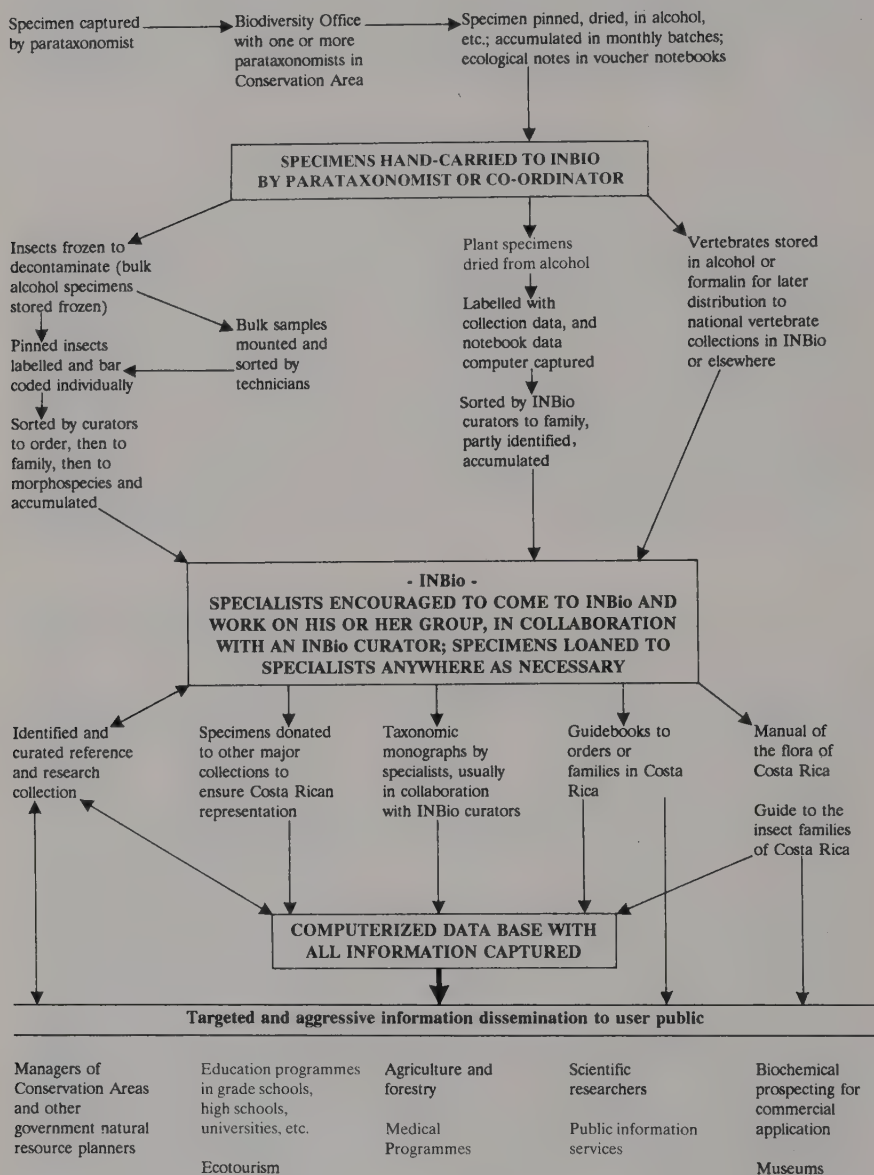


Fig. 15.1 Inventory flow of specimens and information from the field through INBio to users.

not only to Costa Rica, but probably to all countries throughout the isthmus of Central America. The Costa Rican pimpline fauna can now be said to be as well known as that of the United States. Although most of the holotypes of the 118 new species described in Gauld's monograph are deposited in INBio, representative collections of the Costa Rican fauna are deposited in leading British and North American institutions.

Beginning to Use Biodiversity

The flow of specimens and information from field to INBio and to users is shown in Fig. 15.1. Data about the specimens and associated biological information accruing at INBio are entered into the National Biodiversity Database, then specimens are deposited in the Costa Rican National Collection. INBio is experimenting with an innovative system in which every single entomological specimen is given a bar-code label corresponding to a serial number to allow rapid and efficient access to information in the database. This system will eventually be adapted to the other collections of organisms held at INBio as they too are gradually computerized. Thus information on the identity, geographical distribution, natural history, and known and potential uses of all organisms is gradually accumulating into a Biodiversity Information Management System. Conceptually the information in the system will be organized in a format that will make it easily accessible to those using it for intellectual or economic purposes. A central public information unit is being established for the purpose of disseminating the biodiversity information and promoting its use by a wide array of sectors of society, such as those involved in ecotourism, education and science, agriculture and forestry, industry, national planning, conservation and many others.

An example of this approach is a chemical prospecting project for the systematic screening of Costa Rican organisms, funded by the MacArthur Foundation, which is being implemented by INBio, the Universidad de Costa Rica and the Universidad Nacional de Costa Rica in collaboration with Cornell University in the United States and Strathclyde Drug Research Institute in the United Kingdom. The project aims to detect natural products of commercial interest, and to promote the utilization of these products through equitable partnerships with the developed world in ways that guarantee a fair distribution of the profits. INBio has also completed a technical and legal agreement to supply a major international pharmaceutical company, Merck, with specific natural products from plants, insects and environmental samples for the purposes and under the terms described above.

The order Hymenoptera comprises many species of potential commercial interest. A very wide range of chemicals (here referred to as 'venoms') are produced by glands associated with the female reproductive tract and the ovipositor (or sting). Considerable attention has already been paid to the chemical composition of the venoms of many social aculeates (Blum, 1981; Piek, 1986),

although pharmacological study of venoms of tropical species lags far behind the study of the comparatively impoverished temperate fauna. Venoms of the solitary aculeates and the vast array of parasitoids have, in general, hardly been investigated at all, possibly because of the difficulty of collecting and identifying material. Venoms and other secretions of the parasitic Hymenoptera would seem to offer a particularly lucrative area for investigation as substances injected by parasitoids into their hosts are known to have profound physiological effects, including altering growth rates, preventing ecdysis and suppressing immunodefensive systems (Gauld and Bolton, 1988; Vinson, 1990). Larvae of some temperate parasitoids are known to produce substances that have antibiotic effects (Führer and Willers, 1986). Tropical relatives of such species are, because of the activities of INBio and its collaborators, relatively easily collectable, and taxonomically well documented (Gauld, 1991).

Another area where Hymenoptera are potentially commercially important is in biological control. For over a century scientists from industrialized countries and elsewhere have appropriated natural enemies from different regions of the world. These actions have, thus far, been conducted without compensation for donor countries, despite the fact that savings accruing from biological control projects to agriculturists in the developed world have totalled millions of dollars (Altieri, 1991). For example, the combined savings to the State of California's agricultural industry from seven major biological control programmes conducted between 1928 and 1979 have been estimated as about US\$320 million (van den Bosch *et al.*, 1982). As new forestry and agricultural areas are developed, new insect pests are likely to appear. Information about their potential natural enemies, which will be accumulated in Costa Rica's National Biological Database, can then be used in the development of biological control programmes, and a fair share of the financial rewards from savings made in other countries can be channelled back into conserving Costa Rica's biotic diversity.

The Future

The profits from INBio's commercial ventures will be used to ensure the conservation and management of Costa Rica's wildlands and biotic resources in perpetuity. It is envisaged that this innovative approach adopted by INBio may enable Costa Rica to become one of the first countries to implement a national programme for the sustainable utilization of its biodiversity. Even if INBio receives a mere 2% of royalties on pharmaceuticals developed from Costa Rican biodiversity, it would take only 20 drugs for INBio to be generating more funds than the country currently earns from bananas and coffee – its two principal exports (WRI, IUCN, UNEP, 1992).

The international attention attracted by this Costa Rican undertaking (e.g. Tangley, 1990; Hovore, 1991; WRI, IUCN, UNEP, 1992), and the number of delegations and fact-finding groups visiting INBio headquarters from other trop-

ical nations, suggests that the INBio paradigm may spread. Whether the developed world's declining population of biosystematists (e.g. see Holden, 1989; Gaston and May, 1992) can sustain such initiatives until tropical nations have fully developed their own systematic bases remains to be seen. But a direct involvement of this community in conservation efforts of the nature described above may help to improve their future prospects.

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Appendix: Higher Categories of Hymenoptera

The table shows estimated numbers of described species, common names and principal modes of development.

Taxa	Species	Common name	Mode of development
SUBORDER SYMPHYTA	6016	SAWFLIES AND HORNTAILS	
XYELOIDEA	56		
Xyelidae	56	no common name	phytophagous
MEGALODONTOIDEA	302		
Pamphiliidae	232	leaf-rolling and web-spinning sawflies	phytophagous
Megalodontidae	70	no common name	phytophagous
TENTHREDINOIDEA	5328		
Blasticotomidae	9	no common name	phytophagous
Argidae	812	no common name	phytophagous
Cimbicidae	131	no common name	phytophagous
Diprionidae	125	conifer sawflies	phytophagous
Tenthredinidae	3840	common sawflies	phytophagous
Pergidae	411	no common name	phytophagous
SIRICOIDEA	182		
Siricidae	87	horntails	phytophagous
Xiphydriidae	94	wood wasps	phytophagous
Anaxyelidae	1	incense-cedar wood wasps	phytophagous
ORUSSOIDEA	69		
Orussidae	69	parasitic wood wasps	parasitoid
CEPHOIDEA	79		
Cephidae	79	stem sawflies	phytophagous
SUBORDER APOCRITA	109833		
PARASITICA	55641	PARASITIC HYMENOPTERA	
TRIGONALYOIDEA	70		
Trigonalyidae	70	no common name	parasitoid
MEGALYROIDEA	< 100		
Megalyridae	< 100	no common name	parasitoid
EVANIOIDEA	1050		
Evaniidae	400	ensign wasps	parasitoid
Aulacidae	150	no common name	parasitoid
Gasteruptiidae	500	no common name	parasitoid
STEPHANOIDEA	> 100		
Stephanidae	> 100	no common name	parasitoid

Taxa	Species	Common name	Mode of development
CERAPHRONOIDEA	802		
Megaspilidae	448	no common name	parasitoid
Ceraphronidae	354	no common name	parasitoid
PROCTOTRUPOIDEA	2597		
Pelecinidae		no common name	parasitoid
Vanhorniidae		no common name	parasitoid
Roproniidae		no common name	parasitoid
Peradeniidae	45	no common name	not known
Heloridae		no common name	parasitoid
Austroniidae		no common name	parasitoid
Monomachidae		no common name	parasitoid
Proctotrupidae	310	no common name	parasitoid
Diapriidae	2242	no common name	parasitoid
PLATYGASTEROIDEA	4022		
Scelionidae	2922	no common name	parasitoid
Platygasteridae	1100	no common name	parasitoid
CYNIPOIDEA	3290		
Ibaliidae	10	no common name	parasitoid
Liopteridae	80	no common name	parasitoid
Figitidae	300	no common name	parasitoid
Eucoilidae	1000	no common name	parasitoid
Cynipidae	1700	including: gall wasps	phytophagous, parasitoid
Charipidae	200	no common name	parasitoid
CHALCIDOIDEA	18610		
Leucospidae	134	no common name	parasitoid
Chalcididae	1466	no common name	parasitoid
Eurytomidae	1201	including: seed chalcids	parasitoid, phytophagous
Torymidae	889	no common name	parasitoid, phytophagous
Agaonidae	608	fig wasps	phytophagous
Ormyridae	66	no common name	parasitoid
Eucharitidae	348	no common name	parasitoid
Perilampidae	229	no common name	parasitoid
Pteromalidae	3003	no common name	parasitoid
Eupelmidae	715	no common name	parasitoid
Tanaostigmatidae	88	no common name	phytophagous
Encyrtidae	3277	no common name	parasitoid
Tetracampidae	44	no common name	parasitoid
Aphelinidae	975	no common name	parasitoid
Signiphoridae	75	no common name	parasitoid
Eulophidae	3346	no common name	parasitoid, phytophagous
Elasmidae	203	no common name	parasitoid

Taxa	Species	Common name	Mode of development
Trichogrammatidae	630	no common name	parasitoid
Rotoitidae	1	no common name	not known
Mymaridae	1 303	fairyflies	parasitoid
Mymarommatidae	9	no common name	not known
ICHNEUMONOIDEA	25 000		
Ichneumonidae	15 000	no common name	parasitoid
Braconidae	10 000	no common name	parasitoid
ACULEATA	54 192	WASPS, BEES, ANTS	
CHRYSIDOIDEA	4 899		
Plumariidae	20	no common name	parasitoid
Scolebythidae	3	no common name	parasitoid
Sclerogibbidae	15–20	no common name	parasitoid
Dryinidae	844	no common name	parasitoid
Embolemyidae	12	no common name	parasitoid
Chrysididae	3 000	cuckoo wasps	parasitoid
VESPOIDEA	21 593		
Tiphidae	1 500	no common name	parasitoid
Mutillidae	3 500	velvet ants	parasitoid
Sapygidae	80	no common name	parasitoid
Scoliidae	300	no common name	parasitoid
Bradybaenidae	200	no common name	not known
Sierolomorphidae	10	no common name	not known
Rhopalosomatidae	33	no common name	parasitoid
Formicidae	8 800	ants	predator, phytophagous
Pompilidae	2 000–3 000	spider wasps	predator
Vespidae	4 170	including: paper wasps, yellow jackets, hornets, mason wasps, potter wasps	predator
APOIDEA	27 700		
Sphecidae	7 700	including: mud daubers, sand wasps, bee wolves, cicada killers	predator
Apidae	20 000	bees	pollen (plus nectar or oil) feeders
Total	> 115 000		

Source: Compiled from Tables 1.1 and 12.5.

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HYMENOPTERA AND BIODIVERSITY

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Increasing attention has been focused on biodiversity in recent years, based on a number of arguments to justify the conservation of the world's flora and fauna. Such arguments may be economic – that species may have potential for food or medicine – or ecological – that the extinction of any species affects the overall ecological balance. Little attention, however, has been focused on which groups have the greatest impact on maintaining diversity.

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